Short-term task allocation in small social insect groups

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SHORT-TERM TASK ALLOCATION IN SMALL SOCIAL INSECT GROUPS

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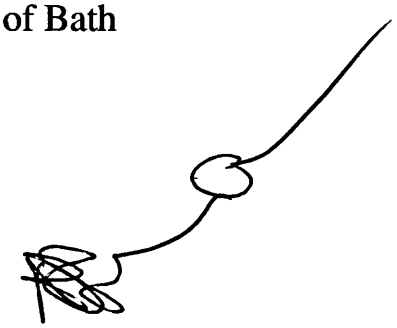

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Summary

I argue that available empirical evidence points toward fundamental differences between task allocation that occurs in the short term, over time scales of minutes to hours, and that which occurs over time scales of days or longer. Most social insect species fit a pattern of two to four 'roles', characterised by increasing risk, through which workers tend to progress over the course of their lives, and workers may switch on shorter time scales between the tasks within one role. Accordingly, I propose the terms 'between-role' and 'within-role' for long- and short-term task allocation, respectively. In addition, task allocation in small groups has to meet different requirements from task allocation in large groups with regard to managing stochasticity, and can therefore be expected to employ different mechanisms.

Empirical studies and models of task allocation are reviewed. Short-term task allocation in small groups is poorly understood: although the phenomenon of short-term flexibility within a role has been clearly demonstrated, the mechanisms underlying it are not known. In modelling, there has been too little attention given to making testable predictions, and consequently despite a number of models having been published, little work has been done to test them experimentally.

Two case studies are reported. One is a model of short-term task allocation based on propensities for responding to task stimuli, where a worker's propensity for a task is reinforced when it works on an item of that task. The behaviour of this model is explored and some potential experimental tests suggested. The second is an empirical study of a specific task: the fetching of wall material to the nest in the ant *Leptothorax albipennis*. The profile of workers that perform the task and the factors that induce task performance are tested.

Finally, suggestions for future work that arise from these studies are discussed.

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« Qu'un moulinet de leurs grands bras chargés de toiles
Vous lance dans la boue!
—Ou bien dans les étoiles! »)

Chapter 1

Introduction

1.1 Why study social insect task allocation?

The purpose of this study is to learn how task allocation in multi-agent societies can be made effective by investigating how social insects have solved the problem of short-term task allocation in small colonies.

The potential value of the work presented is threefold.

First, multi-agent systems are among those that have proved most resistant to (predictive) understanding. Many collective manifestations in human behaviour come under this heading, from economics (Krugman, 1996; Cliff, 1997) to crowd movement (Couzin, 1999). Further examples come from collective phenomena in many other organisms: flocking/shoaling behaviours (e.g. Warburton & Lazarus, 1991; Gueron *et al.*, 1996; Couzin, 1999), predator–prey and host–parasite systems (Murray, 1993; Capasso, 1993), and indeed systems at the sub-organismal level such as our own immune system (e.g. Kauffman, 1989) and nervous system (e.g. Segev & Ben-Jacob, 1998) and even, in a looser sense, the genome (in the sense that it is a network of interacting elements: Lyubich, 1992; Nagylaki, 1992). If we can better understand how multi-agent systems operate and can be regulated, we may be able to use the principles learned to advantage in various areas of human enterprise, much as many previous structures and devices of human invention have been anticipated by biological ones built on the same principles (vision, Harris & Jenkin, 1993 and Cantoni, 1994; sonar

Fay, 1995, and in dolphins, Au, 1993; cantilever structures and logarithmic spirals, Thompson, 1942; and a medley of other structures, von Frisch, 1974). In these past examples, human invention has often been echoing natural designs unwittingly and the parallels have only later come to light (most notably in the case of sonar: Au, 1993, Chapter 1). It would be good if future parallels between biology and engineering could be identified in time to be useful, rather than after the fact.

One example of the type of multi-agent system that might be useful to humans is that teams of robots could be used to reduce exposure of humans to risk by carrying out work in dangerous environments—a process already well advanced where single machines are concerned but which could be taken into new domains with an ability to manage group-level behaviours. Such possibilities for physical multi-agent groups are as yet distant, but it is hoped that a better understanding of social insect task allocation would bring them a little closer. However, there is no reason to limit such societies to groups of entities with physical bodies; software agents are already becoming common, and computer networks could be seen as societies of software agents, particularly with regard to network routing (Schoonderwoerd *et al.*, 1996; Subramanian *et al.*, 1997). Societies of software agents may also be used to solve more abstract problems: see Bonabeau *et al.* (2000) for a review and Dorigo & Gambardella (1997) for a specific example of mathematical algorithms strongly inspired by social insects.

Second, a more specific and biological benefit of studying (proximate) mechanisms of task allocation in particular social insect species is that it leads to an improved understanding of the involvement of division of labour in the evolution of social insects and hence of the roots of their ecological dominance (Wilson, 1987). Social insects are an extremely important part of most terrestrial ecosystems, and therefore understanding them better can be helpful in managing and conserving those ecosystems (e.g. army ants: Partridge *et al.*, 1996; Boswell *et al.*, 1998). In other situations, social insects have become successful to the extent of being pests, and we may wish to understand them better for less benign reasons. In either case, the division of labour is central to the study of social insects (Oster & Wilson, 1978), and understanding it is the vital to understanding them.

Third, with regard to the work presented here that investigates a real organism, I hope that it may be accepted that learning about any of the species which exist on this planet is a thing of value in itself and which is justified without recourse to any positive effects it may subsequently have on biologists or on any other humans.

1.1.1 Why concentrate on small groups?

I discuss in more detail the differences between small and large groups, and those between short- and long-term task allocation, in the following chapter. The following is an extremely brief resumé.

Small groups present different problems to large groups—stochastic effects are far more important in small groups, while collective pattern is less complex—and are easier to study both in the laboratory and on computer because the smaller scale and numbers involved demand fewer resources. Additionally, small groups are more likely to be found in human-built analogues of these processes (e.g. teams of robots), at least in early stages.

1.1.2 Why concentrate on short-term task allocation?

There is evidence that social insects themselves use different strategies to manage long-term and short-term task allocation, as will be discussed in the following chapter. Thus they merit being considered separately. Of the two, long-term task allocation has been the better studied, whilst short-term task allocation probably resembles more the problems that might be relevant to human-constructed agent societies.

1.2 Outline

My intention in this thesis is, first, to review available evidence on task allocation in social insects, and to discuss previously published models; second, to present modelling work offering some further insights and to compare it to available empirical information; and third, to examine a specific short-term task in a particular species, learning about its regulation, with regard to what has been found in the other sections.

Thus Chapter 2 reviews the published literature on task allocation and division of labour in social insects, particularly as it concerns short-term task allocation in small groups, but also drawing comparisons with longer-term task allocation and/or well studied larger societies such as the honeybee. It also provides a critical review of ex-

isting theoretical models of task allocation—critical in that the assumptions and the limits of applicability of each are examined. Chapters 3 and 4 explore a model of one possible mechanism for short-term task allocation. Chapters 5 and 6 investigate a specific case study, the fetching of material for wall construction in the ant *Leptothorax albipennis*. Finally, Chapter 7 provides a closing summary and some overall conclusions.

Chapter 2

Task allocation literature review

2.1 Definitions

Before discussing what is known about how short-term task allocation operates in relation to long-term task allocation, and why or how small groups differ from large ones, it is appropriate to give some indication of what is meant by 'short-term' and 'small'.

2.1.1 'Short-term'

A term can only be defined in relation to other terms. Since the terminology of task allocation has been the subject of some controversy (Robinson *et al.*, 1994; Franks & Tofts, 1994; Traniello & Rosengaus, 1997; Robson & Beshers, 1997; Franks *et al.*, 1997, and see below), it is necessary to outline the issues involved, so as to ensure that the definition itself is clear.

The knowledge that social insect workers of different ages tend to perform different tasks is widespread and of long standing. Aristotle famously made some remarks on the subject (cited in Bourke & Franks, 1995, p. 401); as far as modern times are concerned, Moritz & Page (1999) attribute the idea to Rösch (1927, 1930). Controversy stems from the question of whether workers' task performance can or should be

described as age-determined, and whether terms that suggest so should be used. An association between two variables may be found, as has been done for worker age and task performance (for reviews see e.g. Hölldobler & Wilson, 1990; Robinson, 1992; Bourke & Franks, 1995, chapter 12), but showing that one causes the other is quite another matter. Nonetheless, it has long been held that the association between age and task is causative, leading for example to the concept of 'adaptive demography' (Wilson, 1985; Hölldobler & Wilson, 1990, pp. 307–310) where the age structure of a colony is seen as an adaptive trait optimised by natural selection. Reflecting this view, the terms 'age polyethism' and 'age-based division of labour' have been widely used to describe either the association between age and task, or the division of labour which is presumed to arise through task being determined by age.

Tofts & Franks (1992) and Tofts (1993) challenged such thinking by publishing a model of task allocation (the 'foraging-for-work hypothesis', or FFW) in which an association between age and task could emerge without an individual actually using its age to determine its choice of task (a description of the model is given on p. 37). They also argued that a division of labour adjusted through natural selection over evolutionary time scales would not be sufficient to meet the day-to-day fluctuations experienced by many social insect colonies, and pointed out that it has not been convincingly shown that worker task choice in any social insect species is *determined* by worker age (see also Franks & Tofts, 1994; Bourke & Franks, 1995; Franks *et al.*, 1997).

In the honey bee—probably the best studied social insect species, due to its commercial importance—whilst workers usually experience a progression from being 'nurse' bees (brood care, queen attendance) to being 'hive' bees (undertaking, building, receiving incoming forage, guarding) to foraging, each stage can be prolonged or curtailed according to the hive demography (shortage or surplus in any of these groups) and workers can even revert from a 'later' stage to an 'earlier' one (see Robinson, 1992; Huang & Robinson, 1999 for reviews). These phenomena are seen not only under artificial laboratory manipulation but in natural conditions, as for instance following colony fission when the departing swarm, by the time that new brood emerge as adults, consists entirely of older bees, some of which are obliged to remain nurses (Robinson *et al.*, 1989). Juvenile hormone (JH) appears to be involved in the regulation of this process (reviewed by Huang & Robinson, 1999), as foragers have higher levels than workers within the hive. However, it remains unclear exactly how JH is involved: it is not the determining factor, as JH level itself is affected by worker-worker interactions (Huang & Robinson, 1992). It was proposed by Huang & Robinson (1992; see also

Huang & Robinson, 1999) that an activator-inhibitor model could account for these observations, and a simulation (Naug & Gadagkar, 1999) based on their word model is discussed later in this chapter.

Thus, whilst the honey bee worker might be considered to have an age-based programme by default, this programme is highly flexible and easily modified according to circumstances. Other species have been less well studied: associations between age and task are widespread (Wilson, 1971; Hölldobler & Wilson, 1990; Jeanne, 1991) but there is little indication of a rigid determination of task by age, especially since the association is in many cases a rather loose one (sometimes referred to as 'weak age polyethism'). It is highly likely that a similar picture obtains in many of these species. Indeed, such detailed investigations as have been carried out (e.g. on the ant species *Leptothorax unifasciatus* and *L. albipennis*, in which task is loosely associated with age: Sendova-Franks & Franks, 1993, 1994, 1995; Backen *et al.*, 2000) tend to support this view.

Consequently, there has been a shift in emphasis over recent years from the adaptive demography approach and an interest in discrete castes fixed either through age or through morphological differences (e.g. Wilson, 1968, 1976; Oster & Wilson, 1978) towards an interest in colony mechanisms of flexibility and adaptibility and their basis in individual behaviour. The shift is not a rejection of earlier work but an adjunct to it, and a typical view today (Bonabeau & Theraulaz, 1999) might be that colonies evolve to have both default parameters that optimise performance under typical conditions, and mechanisms to respond to fluctuation by adjusting the balance of workers engaged in different tasks.[1]

This picture of a default state which may in practice often not be realised raises the question of how it is appropriate to describe the stages in the behavioural programme and the progression, or otherwise, through them. The term 'age-based division of labour' has lately been replaced by 'age-related division of labour' or 'temporal polyethism', yet even these are not entirely satisfactory. They may be adequate for describing the age/task profile of the colony as a whole, if workers of different age cohorts perform different tasks, but I am unconvinced that they are appropriate for describing the task choices of individuals, if those workers' task choices are not *primarily*, or even

[1]That is not to say, as Bonabeau & Theraulaz (1999) point out, that conflict might not exist between the two levels of selection. For instance, as mentioned later in this chapter, under some conditions it may be adaptive on an individual level for younger workers to remain in the nest, which could conflict with colony-level selection for behavioural flexibility.

(as FFW shows is possible) not at all directly determined by their age.

Age is an absolute measurement of the time elapsed since eclosion, or some other suitable starting point. The expression 'physiological age' as something distinct from real or 'chronological' age (proposed by Robinson *et al.*, 1994, who argue that "temporal polyethism in social insects is a developmental process,") is misleading (Franks & Tofts, 1994). How can the word 'age' indicate anything other than chronological age? Similarly, to refer to worker task choice as 'behavioural development', with its analogy to metazoan development and implication of an unidirectional change regulated by internal impulses, is not ideal. A preferable term to these would refer to the stages of a worker's life without implying that those stages form an immutable progression nor that age plays the principal role in task determination.

For this reason I prefer the terminology proposed by Blanchard *et al.* (2000). They suggest that each stage in this reversible progression be described as a 'role'. A role comprises several tasks, and individuals may switch between tasks whilst remaining in the same role.

We can now appreciate the distinction between short-term and long-term task allocation: long-term task allocation is the allocation of workers to different roles, and short-term task allocation is the allocation of workers to tasks within a role. Figure 2.1 shows how tasks would be divided into roles in a representative example species. Blanchard *et al.* (2000) refer to short-term task allocation as 'task switching', but when the distribution of workers among the tasks within a role is stable, switching will not happen; yet this does not mean that there is no allocation. Hence I prefer the label 'within-role task allocation'. In this thesis, 'within-role task allocation' will be used interchangeably with 'short-term task allocation', and 'between-role task allocation' with 'long-term task allocation'.

The distinction made by Blanchard *et al.* (2000) between roles and the tasks within a role has also been noted by other authors. Jeanne (1986b) was "particularly interested... to analyze task partitioning, or specialisation over the short term (several days or less) (Jeanne, 1986a), rather than division of labor in the usual sense."[2] Gordon (1996) comments that, "From day to day, or even hour to hour, an individual worker may...

[2]He does, though, confound the distinction between short- and long-term task allocation with the distinction, made in Jeanne (1986a), between focusing on how a worker's time is divided between tasks (task allocation) and on how a task is divided among workers in its successive stages (task partitioning); see also Ratnieks & Anderson (1999a).

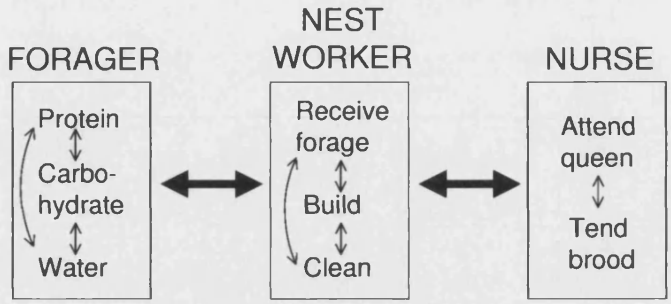


Figure 2.1: Scheme for differentiation between and within roles. The scheme is purely illustrative: some species may have two or four roles, different foraging specialisations, and so on. Nonetheless the arrangement given is intended to be typical, and a substantial proportion of species should fit it. Bold arrows denote between-role transitions which are expected to take place over a period of days or longer as physiological changes may often be involved. Light arrows denote task switching within roles, taking place over periods of minutes or hours.

[change] its task as circumstances require. (Note that task switching here refers to a more rapid shift in task than those, on the scale of weeks or months, that lead to age polyethism.)" Similarly, on honey bees, Page & Robinson (1991, pp. 129-130) state: "There is also inter-individual variation in the degree of task specialization within [a role]," and proceed to give several examples.

What evidence is there that this distinction is a genuine one? It would be a genuine distinction if the two were operated by different mechanisms—in other words, if it is seen as a distinction not only by ourselves but by social insects themselves. Whilst the picture is far from complete, available evidence indicates that such is indeed the case. As discussed above, in honey bees there appears to be a reversible progression through roles in the regulation of which JH is involved. By contrast, it seems that task choice *within* a role involves genetic factors (for instance, between guarding and undertaking, two behaviours that occur at about the same age; Robinson & Page, 1988). This is not to suggest that genetic factors are the only ones of importance: whether an individual performs a task, genetically predisposed to it though it may be, could also depend on the extent to which the need for it is already being met by other workers (Seeley, 1995; Beshers *et al.*, 1999). Some have suggested that the existence of extreme polyandry in the honey bee can be attributed to an effort to ensure the presence in the colony of rare but important 'specialist genotypes', carried by a small proportion of drones (Fuchs & Moritz, 1998), although it should be noted that this hypothesis is not entirely uncontroversial. In any case, the involvement of genetic factors shows that task allocation over different time scales is managed in different ways in the honey bee.

In the ant *Leptothorax albipennis*, the species studied in some of the following chapters, Blanchard *et al.* (2000) found that corpulence was involved in the determination of role. Clearly patterns of corpulence cannot change in response to day-to-day changes in task demand; therefore other mechanisms must be responsible for within-role task switching. Incidentally, as mentioned above, *L. albipennis* shows weak temporal polyethism, and the study of Blanchard *et al.* (2000) again shows how such an association might arise not so much through age determination but rather as the outcome of an interaction between seasonal fluctuations in task demand, the production of new workers, and worker mortality.

That within-role task allocation should be treated separately from the division of labour between roles is also in keeping with theory for many species. The organisation of labour into different roles is fundamentally a grouping together of tasks with similar levels of risk. West-Eberhard (1979) observed that, when workers can reproduce, they have an incentive to remain in the nest to maximise their egg-laying opportunities whilst young, rather than risking an early death by venturing outside. Naturally this argument does not apply in the many cases where, for physiological or behavioural reasons (worker policing), workers are unable to produce eggs of their own (Bourke & Franks, 1995, pp. 405–406), but under the right conditions there can be colony-level selection where the colony as a whole benefits if older workers perform the riskier tasks, as this maximises the average amount of work that each is able to do for the colony (Wakano *et al.*, 1998). Needless to say, neither argument can apply to tasks with similar degrees of risk. Therefore, in the many species which meet their conditions, division of labour between roles needs a mechanism that shelters younger workers from risk under normal conditions but can respond to abnormal conditions, whereas allocation of workers to tasks at the same level of risk can proceed without regard to such considerations.

2.1.2 'Small'

The other tenet of this thesis that requires definition is what is meant by a 'small' group. As concrete a definition of this term cannot be given as was done for 'short-term task allocation' because there is, of course, no demarcation between small and large groups but a continuum of sizes. Furthermore, it is not the size of the colony as a whole that determines what task allocation mechanism is suitable for a specific task, but the number of workers that the task requires, the size of the pool from which they are to

be drawn, and the number and nature of the other tasks competing for the attentions of that pool. As the preceding section makes clear, whilst workers may switch tasks readily within a role, transfer between roles is expected to be a slower process (on a time scale of days or weeks rather than minutes or hours), and so the pool of workers available for a task is likely to comprise not the entire set of unoccupied workers in the colony, but only the unoccupied workers within the same role.

The reason for concentrating on one portion of the size scale is that different sized groups do not have the same properties, nor do they face the same challenges. In groups numbering many hundreds, or especially thousands and tens of thousands, there is a possibility for mass action and collective pattern which simply cannot occur below these sizes—as an example, the swarm raids of army ants (Deneubourg *et al.*, 1989; Franks *et al.*, 1991) or the immense structures built by termites (Smeathman, 1781; Grassé, 1959; Bonabeau *et al.*, 1998b). In such collective patterns, the structure arises not from independent individual decision making but from interactions, direct or indirect, among workers. This is not to say that the group behaviour is not the outcome of all the individual behaviours, but that the processing of information about conditions is a property of the group and not of individuals, because most individuals in these large groups are getting most of their information from nestmates rather than directly from the environment (as presaged by Wilson & Hölldobler, 1988). As groups get smaller, workers are more likely to be independent in their gathering and evaluation of information (Franks, 1999). Social complexity may also be less in small colonies for reasons to do with kin selection and conflict (Bourke, 1999).[3]

The other important difference between small and large groups is that small groups are much more susceptible to stochasticity. If workers die at random, and are replenished at a regular rate, the size of a small group will be less predictable than that of a large one. Consequently an inflexible task allocation, determined over evolutionary time scales, is less likely to be effective in small groups; some degree of adaptability to the vicissitudes of chance is likely to be needed. Aside from the purely stochastic effects of worker mortality, which affect the size of the group available to perform tasks, there are environmental changes that affect the amount of work it has to perform. Large colonies equally experience these changes, but are better able to exploit the virtues of being 'factories within fortresses', having more potential to buffer against external

[3]Bourke (1999) describes as 'small' colonies with an upper size limit of 100 or less, and as 'large' those with an upper size limit of 1000 or more (to the nearest order of magnitude) whilst Franks (1999) uses 'large' and 'small' to refer to colonies "with a maximum of more than 1000 workers or with a maximum of about 100 workers or less, respectively."

changes (Oster & Wilson, 1978). The interior of a large colony almost becomes an independent world for the workers in it. There is therefore a justification for studying small and large groups separately, as well as for comparing the two.

For these reasons, the focus of the work here is on tasks performed by one or two up to ten or twenty individuals, drawn from pools of around ten to around one hundred. (These figures should be taken as a very approximate guide.) As well as large groups, it thus excludes *very* small groups, because, whilst being interested in small groups, I wish to omit the case where a group is so small that each member can have good information most of the time on what the other group members are doing. The extreme case is that of a single individual, which always (obviously) has complete information about what it does, and which never has to select tasks with reference to the choices made by co-workers. It is precisely the fact that an optimal task choice depends not only on what needs doing, but on what other members of the group are doing, that makes task allocation an interesting problem (Detrain *et al.*, 1999).

2.1.3 Summary

Short-term task allocation in small groups, on the basis of the preceding argument, is expected to divide workers in a role among the tasks requiring attention within that role, and to be responsive, adjusting the balance when task demand changes or when numbers engaged in a particular task change due to mortality. It is not expected to involve an age-based component.

2.2 Empirical evidence

Let us now turn to a consideration of available empirical data that may shed light on short-term task allocation in small groups. To begin with a contrasting example, it has been suggested (as mentioned above) that within-role task allocation in honey bees may be due to genetic diversity within the colony (emanating from the queen's use of sperm from many drones). A honey bee colony is quite large (typically 25 000 workers; Seeley, 1995) and such a strategy depends on the 'law of averages': by taking a large enough sample, one is fairly sure to get something of everything. Even if

this is the strategy employed by honey bees, it would not work for a smaller group: there would be too much risk of missing some essential specialist genotypes (Fuchs & Moritz, 1998). Within-role task allocation, or 'task switching', has been studied in seed harvester ants by Gordon (1989). Again, these colonies are large groups (up to 10 000 workers per colony; MacKay, 1981, cited in Gordon, 1989); however, whilst the mechanism has not been established, Gordon showed that adjustments in levels of task effort could be made in response to (artificially manipulated) changes in task demand. Indeed the clever manipulations used to stimulate demand are exactly the approach that is needed for studies on short-term task switching. It may transpire that whatever mechanism the harvester ants use would be suitable for smaller groups also. However, Gordon (1999) suggests that regulation in these groups may occur through mass interactions: workers gain information about task demands and colony activity not through direct evaluation of task stimuli but by receiving information from individuals they encounter about what tasks those other individuals have been engaged in (see also the model of Pacala *et al.*, 1996). Whilst its existence has not yet been convincingly demonstrated, this hypothetical mechanism, if correct, might not apply to small groups, given its element of mass action. That is, it relies on small individual samples from large numbers of individuals being integrated through inter-individual interactions, whereas the tendency in small groups (presumably because such a strategy becomes unreliable when numbers are small) is for individuals to do all their sampling themselves and to carry out independent decision making (Franks, 1999, and see above).

Jeanne (1986b) studied divisions between water foragers, pulp foragers and builders, probably a case of within-role task allocation, in the eusocial wasp *Polybia occidentalis*. In this case, both large groups (> 350 adults) and small groups (< 50 adults) were studied. (Colonies are swarm founded, but small ones can occur due to predation of brood.) It was found that there was more switching in smaller groups, which was attributed to the greater influence of stochastic variability. These results are further discussed in section 6.4 (p. 142); suffice it to say here that, when material is being transferred directly between workers as part of a task, queueing delays experienced may be used by both donors and recipients as cues assisting in task choice (Ratnieks & Anderson, 1999a). However, workers in small colonies will tend to spend a greater proportion of their time queueing, increasing the probability that switching (i.e. a donor carrying out the recipient's task itself instead of waiting to find a recipient) becomes the more profitable option (Anderson & Ratnieks, 1999a; Ratnieks & Anderson, 1999a).

Studies on division of labour in smaller groups have concentrated more on between-role task allocation than on within-role task allocation. As previously mentioned, Blanchard *et al.* (2000) found results indicating an involvement of corpulence in between-role task allocation in *L. albipennis*. Sendova-Franks & Franks (1993, 1994, 1995) found an association between task and spatial location in the sister species *L. unifasciatus*, which has similar nesting habits and colony size to *L. albipennis* (Sendova-Franks & Franks, 1993). Their categorisation of tasks is fine-grained enough to include ones that might belong to the same role as each other, but that does not necessarily mean that the association between task and role is equally fine-grained, with all tasks arrayed along a single continuum. Indeed, they found that workers fell into four clusters, corresponding to four spatial stations (Sendova-Franks & Franks, 1993), which is rather consistent with the scheme of roles and tasks argued for here. Since the studies were long-term, they can probably be considered as studies of allocation between roles rather than within a role.

On the whole, whilst there have been many studies on aspects of task allocation in a wide range of social insect species, the majority of studies content themselves with describing a pattern, such as the age-task distribution, rather than carrying out manipulatory experiments to discover something about the underlying mechanisms (e.g. Traniello, 1978; Porter & Jorgensen, 1981; Villet, 1990; Masuko, 1996). Furthermore, the majority of these studies examine aspects of longer-term, between-role task allocation. The present need is both for the field to move into a more rigorous, investigative phase (of which there is every sign) and for it to pay more attention to short-term shifts in labour (of which there is rather less).

2.3 Models

I turn now to considering the models of task allocation in social insects that have been published. Most, like empirical studies, can be categorised according to whether they are applicable to between-role or within-role task allocation. Two, being especially abstract or general, might be applied to either, and are discussed last.

2.3.1 Between-role models

Activator-inhibitor

The progression and occasional regression between roles in honey bees has been the subject of a verbal 'activator-inhibitor' model (Huang & Robinson, 1992, 1999), with the candidate activator being JH, and assumed to accumulate over time and promote progression through roles, and the as-yet-undiscovered inhibitor being some substance transferred between individuals, retarding or inhibiting progression. Naug & Gadagkar (1999) developed this verbal model into a simulation. A worker's levels of activator (A) and inhibitor (I) are coupled and increase throughout its life. Each worker's I does not influence its behaviour, but determines only the amount of I it transfers to other individuals during interactions. The worker's choice of task is determined by its 'A/I ratio', the ratio of its *own* A to the amount of I it receives from *others* during interactions. It is therefore not necessary to posit, as Huang & Robinson (1999) imply, that the inhibitor is literally a specific substance. Since the amount of I a worker transfers to a nestmate during interaction is coupled to its own A, workers could simply be evaluating nestmates' levels of A and inhibiting their progression according to the amount they encounter. Indeed, since activator level, A, is linked to age, it could be replaced in the preceding sentence by 'age', and workers could use any cue linked to age, including but not restricted to JH levels. The fact that JH tracks task suggests that, if the activator-inhibitor model is correct, that JH reflects the A/I *ratio* rather than the level of A itself, and is therefore not a reliable measure of age. The model of Naug & Gadagkar (1999) leads to a division of labour based on 'relative age', which is to say that a workers task choice depends not on its age *per se* but on its age rank (its relative position within the colony's demographic structure.

Some of this confusion is due to the way that Naug & Gadagkar (1999) adapted the verbal model of Huang & Robinson (1992, 1999) in order to get a working theoretical model. Whilst Huang & Robinson (1992, 1999) clearly consider JH to be a candidate activator, the way that it is defined in the model of Naug & Gadagkar (1999) is not consistent with what is known about its involvement in division of labour in honey bees. This does not rule out either JH being consistent with the properties of an activator if the model is formulated differently, or some other activator-like factor being involved (in any case, as Naug & Gadagkar point out, JH does not track role in all social insects as it does in honey bees).

Although the activator-inhibitor model was inspired by work on honey bees, the model of Naug & Gadagkar (1999) is based not on that species, but on the primitively eusocial wasp *Ropalidia marginata*. However it should in principle be adaptable to other insect societies. The main features specific to *R. marginata* seem to be the colony size (25) that was simulated, and the number of roles (3), but the mechanism used looks likely to scale upwards effectively, and the division into three roles is likely to apply fairly widely and besides is probably similarly adaptable.

Optimal age polyethism

Wakano *et al.* (1998) used a model of age-based polyethism to explore under what conditions age polyethism (AP) is advantageous. They used two risk levels (i.e. roles), corresponding to inside- and outside-nest work, and divided a worker's life into 6 stages each of which was associated with a probability of working inside or of working outside the nest. They found that age polyethism was advantageous, in stable conditions, when specialisation within a role enhances performance and/or when mortality is higher than in the outside-nest role. In the latter case, 'hard' AP was optimal, with a precise cut-off between inside-nest and outside-nest work at a particular age. Highly fluctuating conditions tended to promote 'non-AP', that is, no association between age and role. At lower levels of fluctuation they found that 'soft' AP, where the probability of working outside the nest increased gradually in each of the 6 age groups, was the optimal strategy within the constraints of their model. Laudably, they included the effects of fluctuation not only on workload but also on colony demography, pointing out that fewer workers can be produced in times of dearth and that this in turn affects what the optimal age-task relationship might be.

It is important to note that this model shows (under the simplified conditions used) when an *association* between age and role is advantageous. It does not follow that in such cases a strict *determination* of task by age will necessarily occur. The simulation results of Wakano *et al.* (1998) only indicate which of the possible age-based strategies that their formulation permits is optimal under given conditions, but do not show whether some other more responsive mechanism (such as the activator-inhibitor model, discussed above, or response thresholds or foraging-for-work, discussed below) would be still better.

2.3.2 Within-role models

Polyandry in the honey bee

One very simple model is that of Fuchs & Moritz (1998), which is not really a model of task allocation as such but a model of the benefits of polyandry in honey bee queens on the basis of its putative effects on task allocation. It assumes that there exist 'specialist' genotypes within the population whose impact on colony fitness is beneficial when they are expressed at low frequency within the colony's workers, but adverse when they are absent or expressed at high levels. The effect occurs because they cause a worker carrying them to have a greatly increased propensity for carrying out some small but important task—for instance, a hygienic behaviour like corpse removal. It is beneficial for a few workers to do such a task, but adverse if too many perform it since this will be to the detriment of other fitness-enhancing activities. Since the frequency of these alleles in a population will tend towards the frequency at which, as a proportion of a colony, they are beneficial, multiple mating by the queen is advantageous because it improves the sampling of the population and therefore the probability that specialist genotypes will indeed be present in the appropriate proportion of the colony's workers. Aside from being based on rather large assumptions (for instance, that frequencies of these alleles are at equilibrium within the population), this model does not say much directly about task allocation because, even if certain genotypes do have beneficial effects at low frequencies, it does not follow that the effect is necessarily through a strict prescription that workers perform a particular task; it may merely be one among many factors determining its propensity for the task. This is not a *criticism* of the model, which does not seek to explain task allocation, but rather seeks to explain extreme polyandry in the honey bee on the basis of certain assumptions about how task allocation works. Nonetheless, insofar as Fuchs & Moritz (1998) are putting forward a particular view of how task allocation might work, it is worth observing here that such a strategy, whilst not impossible, is less likely to work in small groups precisely because there is more scope for chance variation and more risk of having the specialist genotype expressed among too few—or too many—of the workers. Furthermore, in species where extreme polyandry is not found (of which there are many; Bourke & Franks, 1995) it clearly cannot be occurring.

Distributed network models

Two models describe themselves as distributed network models. Gordon *et al.* (1992) describe a model of the numbers of harvester ant exterior workers in each of eight states. The eight states correspond to activity and inactivity in each of four outside-nest tasks. They use interaction matrices to determine switching decisions between the states. Ants are updated at random by summing the states of other ants, each multiplied by the value at the relevant position in the interaction matrix. The matrices are set up so that, for switching between activity and inactivity, only the numbers of active and inactive workers in the same task as itself affect a worker's decision, and it will become or remain active if inactive workers are in the majority, and *vice versa.* For switching between tasks, only active workers can switch, and their switching depends only on the numbers of active workers in each task. Inactive workers neither switch themselves nor affect switching by others.

The justification given for the assumptions is weak. Strictly speaking, it is assumed that all individuals can in principle interact with all others, but the values in the interaction matrices limit the effect of those interactions to workers in certain states. This is justified as follows: "Though interactions between ants are local [and by pairwise encounter], it appears that movement and random encounters, especially at the nest entrance, lead to enough mixing to warrant [the assumption]... that all ants in a category interact before making a decision." Even if this is true (see p. 31), it does not explain why only the level of activity within its own task can induce a worker to switch between activity and inactivity. Surely an active worker is more likely to encounter active workers of other tasks in the nest entrance and outside the nest than it is to encounter inactive workers of its own task (which, according to the authors, remain inside the nest). Nor does it explain why inactive workers do not use any of the information about levels of inactive workers in the other tasks to decide whether to switch. The authors state, "We assume that there are interactions between active ants only, since no data are yet available on interactions among task groups inside the nest." But lack of data is not a mandate to make assumptions at will. Where the data allow several possibilities, more than one should be explored, and one would like to know in this case what would happen if the assumption that 'inactive' individuals do not interact is relaxed. (Note that they are inactive in the sense of not being engaged in a certain task, rather than of being necessarily immobile.)

Besides the questions over its assumptions—which could easily be countered by mod-

ifying the interaction matrices to explore other patterns of information exchange—the model suffers from a far more serious weakness, which is that it does not consider the effect of task demand on task allocation. Indeed, it does not model tasks at all. Instead it explores the dynamics of numbers in each state based on the numbers in the other states, which each in turn depend on the numbers in all the other states and on nothing else. The interaction matrices used are such that the system tends to a global equilibrium with equal numbers of individuals in each state. The effect of task demand is brought into the model only by introducing 'perturbations', which in fact are non-equilibrium starting conditions. Thus, whilst the model can explore how a perturbation in task demand in one task might propagate through to the numbers of workers engaged in other tasks, it includes no mechanism by which workers can actually respond to task demand, and therefore is lacking a vital element. It also deserves some of the same criticisms as the model described next for failing to offer substantive testable predictions.

A model described as a 'Boolean network model' was presented by Page & Mitchell (1990) and most recently by Page & Mitchell (1998). It consists of the following. A population of workers have randomly distributed thresholds between 0 and 100. If each one's threshold is below the stimulus level, it performs the associated task; if not, it does not. The stimulus level at any given time is equal to its starting level (100) less a fixed amount (1) for each worker that is currently engaged in the task. Three alternative orderings are used for updating workers: all updated simultaneously, updated in sequential order, and updated by selecting workers at random. When all are updated simultaneously, the number engaged in the task oscillates between zero and 100% on successive steps. This is because, on the first step, no workers are performing the task, so all have thresholds higher than the stimulus, so all begin doing it. The next step, all workers are doing the task, the stimulus is consequently reduced to zero (as there are 100 workers), so they all stop. On the following step, the stimulus has gone back to maximal, so they all start again, and so on. The result is clearly an artefact of the updating method and the structure of the model, and it is impossible to imagine what light it throws on real social insect colonies. Yet, far from dismissing it, the authors see it as validating the model: "[In these results] we see the kinds of behaviour long marvelled in insect societies: 1) 'homeostasis' resulting from negative feedback ... 2) 'mass action responses' when all elements turn **on** then **off** when simultaneous sampling is employed" (authors' own emphasis).

The homeostatic effect mentioned in the quotation occurs when workers are updated

not simultaneously but sequentially or randomly. In either case, with each individual that is chosen, since all individuals are inactive as a starting condition the stimulus will usually be above the individual's threshold and so it will be switched on. As more switch on, the stimulus is reduced and so individuals are less likely to have a threshold lower than the stimulus level. Equilibrium and stability is reached when all the individuals with a threshold lower than the stimulus are switched on, and all those with a threshold higher than it are switched off. The model consists of nothing *but* a negative feedback system; it is therefore hardly surprising that it exhibits "homeostasis resulting from negative feedback".

It is unclear what the model aims to describe. Some remarks suggest that the intention is to study the emergence of sociality, yet it is also stated that "honey bees [are] the exemplar organism." Now, honey bee colonies are swarm founded and therefore never resemble the 'proto-society' that Page & Mitchell (1998) claim to simulate. This has a bearing on the starting conditions used: always to have all individuals inactive as a starting condition could apply to a proto-society, but not to a honey bee colony which never is a blank slate.

Other starting conditions could easily be explored. A more serious flaw is that the modelling of task stimuli is quite unrealistic. A real task will usually be decreased permanently when worked on; at the same time it will have a tendency to increase over time if neglected, at a rate reflecting various factors including, potentially, the activity of workers in other tasks. In the model of Page & Mitchell (1998), task does not build up in any such way, and on the other hand workers that perform a task do not consume it; it merely returns to its previous level when the workers stop. It could be argued that task performance cancels out task accumulation to a reasonable approximation in some (though not most) situations, but Page & Mitchell do not attempt any such defence.

The most important criticism, however, concerns the authors' approach to modelling. A model should take available empirical data and use them to make its assumptions as realistic as possible.[4] The model built from these assumptions should then be used to generate new material that adds to the empirical data: details of behaviour which have not yet been studied empirically, for instance, or the effects of manipulations that have not yet been attempted in the real system. Science being commonly thought to proceed through the falsification of or the failure to falsify hypotheses (Shanker,

[4]It should also try to simplify as much as possible, which may conflict with realism. However, there are simplifying assumptions which are broadly realistic, and others which are not.

1996), a model should provide predictions that provide an opportunity to falsify it. Otherwise, publishing the model will not contribute to the stock of knowledge. Since one may be able to imagine more than one way compatible with known data in which a system might work, I would add to the previous duty a duty to provide predictions not only which can be falsified by interrogating the real system, but if possible which distinguish the mechanism modelled from other putative mechanisms.

Page & Mitchell (1998), however, make little attempt to justify their assumptions through recourse to available evidence, nor do they provide testable predictions. Instead they use what is known about the behaviour of real bee colonies to show only that the model's *output* has, in the broadest of terms, similar characteristics to a real colony. No potential is created thereby for adding to our understanding of social insects, as no means is provided by which the model can be verified. These criticisms could also be applied to some other models mentioned in this chapter, but I feel that the one presently under discussion is the best example of how not to proceed.

Self-organisation and local versus global interaction

Some further remarks that apply to both of the models discussed immediately above relate to self-organisation. Self-organisation "is a mechanism for building pattern at the global (collective) level by means of multiple interactions among components at the individual level. The components interact through local, often simple, rules that do not directly, explicitly code for the pattern" (Camazine & Deneubourg, 1994).

Self-organisation has, in recent years, been recognised as a characteristic feature of social insect colonies, and a number of phenomena found in them appear to be self-organised (Bonabeau *et al.*, 1997). It is in the very nature of a self-organised system that it is hard to comprehend the relationship between the local rules followed by its components and the behaviour of the system as a whole, merely by observing the system. Consequently a natural reaction is to try to understand the system's dynamics through modelling.

However, most models that have been produced have actually used global rather than local stimuli. Both of the last two discussed here, for instance, used global stimuli or gave workers global knowledge, although the first laid emphasis on the local nature of interactions in the real system, and the second described itself as a model of self-

organisation. It is not *necessarily* a criticism to observe that the models use global stimuli: clearly, in a social insect colony, some stimuli are global, and so such a model can quite legitimately be applied to them. Indeed, the types of task Page & Mitchell (1998) suggest that their model might relate to in honey bees are ones in which, if stimuli are not exactly global, then individuals can at least accumulate a reasonable evaluation of the global state from the cues available (e.g. the proportion of pollen-containing cells in comb). However, many other stimuli are purely local, particularly interactions of workers with other workers, with brood and with food. A murky area results in which, as with the model of Gordon *et al.* (1992), global interaction is used to model local interaction on the grounds that this "appears" to be a reasonable approximation. Appearances cannot always, though, be trusted. In my view, even if random mixing appears to be taking place, it is dangerous to assume without testing that this is the case. There may well be non-random interaction patterns that are not immediately apparent in the general mêlée.

Worker-worker interactions and task switching

Pacala *et al.* (1996) present an ambitious model of task allocation and task switching in which the behaviour is an outcome of both worker-worker and worker-task interactions. Like the model of Gordon *et al.* (1992), it is inspired by the task switching dynamics of seed harvester ant workers, which Gordon (1999) surmises are driven by worker-worker interactions. However, Gordon *et al.* (1992) *only* modelled worker-worker interactions, as discussed above. The work of Pacala *et al.* (1996) is not an extension of the earlier work, but a completely new model; solely the goal of showing how worker-worker interactions could regulate short-term task allocation is shared between them.

A unique feature of the paper is that the model is validated not by reference to data but by an evolutionary rationale: its behaviour is shown to conform to an ESS. The ESS for task allocation is explained at the start of the paper, and I summarise the explanation here. Each task has some fitness benefit, as well as a cost to performing it. Inevitably, the net effect on fitness of performing different tasks will be different. The ESS is reached when the group cannot increase its fitness by allocating members to different tasks. If there is no density dependence—that is, the per-individual fitness benefit from the task does not change as more individuals perform it—then the ESS is for all individuals to perform the most profitable task. Usually though, there will

be density dependence, so that when many individuals perform a profitable task, the fitness contribution of each individual shrinks with the effect that transferring some to another task might increase group fitness (by increasing the per-capita contribution both of those switched to the subordinate task and of those left in the high-profit task). The ESS has the apparently curious property that the rate at which group fitness would increase if the number of individuals working on a specific task were increased is the same for all tasks that get performed. (In fact this property follows naturally from the preceding statements.) For each task that is not performed, the rate at which group fitness would increase if individuals began to be allocated to it is slower than the rate at which group fitness would increase if extra workers were added to any of the tasks that are being performed. Additionally, of course, the ESS is to not perform a task whose fitness benefit is less than the cost of performing it.

This rate at which group fitness would increase if more individuals worked on task i (which, incidentally, does not include the effect of removing those individuals from some other task) is what Pacala *et al.* (1996) mean by the notation $\mathrm{d}[X_i f_i(R_i)]/\mathrm{d}X_i$, because X_i is the number of individuals working on task i, and $f_i(R_i)$ is the per-individual rate of resource capture, in fitness terms, for task i.

The ESS is the state that maximises fitness, and the rest of the paper consists in developing and exploring a mechanism that is shown to approximate that state. The mechanism has two components, 'dynamics of task switching' and 'dynamics of success', corresponding to two types of state change for workers: workers can switch from one task to another, and within a task they can switch between a 'successful' and an 'unsuccessful' state. Unsuccessful individuals in a given task become successful if they encounter a unit of task resource (being that which is necessary to perform the task), and successful individuals become unsuccessful with fixed probability per unit time if they do not encounter any task resource. Task switching occurs when an unsuccessful individual meets one that is successful in a different task: the unsuccessful individual switches to that task (but remains unsuccessful until it encounters some task resource). Successful individuals do not switch, and unsuccessful individuals do not trigger other individuals to switch. There are also inactive individuals. An unsuccessful individual becomes inactive with fixed probability per unit time if it encounters no task resource, and inactive individuals are recruited to become unsuccessful task i workers if they encounter a successful task i worker. Note that encounters with task resources do not cause task switching, but cause switching between the successful and unsuccessful state within the task. Encounters between individuals are taken as a func-

tion of overall density, but density may be proportional to the group size or there may be some regulation so that density (or at least contact rate) is kept constant as group size increases.

Transitions between the successful and unsuccessful state are explored under three different conditions of resource capture:

1. no density dependence of resource capture probability;

2. density dependence such that the fraction of task i individuals that are successful decreases with the number of task i individuals, and

3. "within-task avoidance of crowding" where a successful task i worker that encounters another task i worker (successful or not) becomes unsuccessful.

It is shown that the last of these classes of behaviour leads to a close approximation of the ESS for a social group. (The other two approximate the ESS that maximises individual fitness). The reason that the ESSs can be approximated in this way is that s_i, the proportion of successful individuals in task i, reflects the rate of resource capture (in units of fitness benefit) for task i. Thus s provides a measure of the fitness benefit of the different tasks, and switching between tasks depends upon s.

The paper goes on to show how colonies of different size track changes in resource capture rate by adjusting the number of workers allocated to each task. Large colonies can make this adjustment more rapidly, but it is shown that if the group regulates its contact rates, having constant contact rates whatever its size, the slowness to respond of a small group is ameliorated.

These are the principal findings of the model as described so far, which is based on a set of deterministic difference equations. A stochastic model is also developed in order to illustrate that it gives good correspondence to the deterministic model, even in some cases with group sizes as low as ten.

I wish to make three criticisms of this paper. The first is that, like several others mentioned, it does not explicitly make testable predictions. As mentioned, it is in a

sense tested by comparing it to the theoretical ESS. Also, a possible test against real organisms can be inferred from the results: experiments could be done to see whether larger colonies really do adjust more quickly to changing task demand. Nonetheless, it would be preferable to have empirically testable predictions made explicitly. The authors are, after all, in the happy position of knowing the model better than anyone else and are therefore best placed to spell out its implications.

The second criticism concerns a limitation in the model, which is the assumption that encounter probabilities reflect global density. In a social insect colony, tasks are not all located in the same place, and so an individual working on a given task is more likely to encounter those working on the same task (e.g. brood care) than those working on some other task (e.g. foraging). The same is true of some other models, including the basic threshold model of Bonabeau *et al.* (1996, and see below) and the model presented in Chapter 3 of this thesis. However, those models implement, without considering spatial heterogeneity, an idea which in principle could be extended to include a spatial element and indeed to some extent has been (Bonabeau *et al.*, 1998a; Chapter 4). The model of Pacala *et al.* (1996) centres around the feature that the fraction of successful individuals in each task reflects resource capture rates and that encounters between successful and unsuccessful individuals in different tasks cause the task allocation profile to match the profitability of each task. Thus, the assumption that encounter probabilities are the same for all group members whatever their current task is not an assumption made to simplify modelling (leaving open the possibility of relaxing it) but a fundamental basis of the model. It is therefore a limitation in a strong sense. Possibly some appropriate behaviour would still happen if it were relaxed, but from my understanding of the model it seems likely that this would inhibit the group from reaching the ESS quickly, and that the effect would be quite severe if the relaxation were at all significant.

The final criticism pertains to the approach taken in measuring fitness. Early on, the authors state, "Let R_i be the abundance of the resource that is the focus of task i... [and] let the function $f_i(R_i)$ be the rate of resource capture by an individual engaged in task i, *but scaled in units of fitness benefit*" (emphasis added). This means that $f_i(R_i)$ is a function that gives the fitness benefit of performing task i for a given resource density R_i. A few pages later comes the remark, "Suppose that an individual captures and processes a unit of resource (R_i) during the small time interval Δt, with probability $k(R_i/\alpha_i)\Delta t$, where α_i is the area over which the task is performed (R_i/α_i is the resource density) and k is [a constant]." Shortly after, it is explained that "$f_i(R_i)$ is the

per capita rate of resource capture, kR_i/α_i."

The implication of these statements is that the model assumes that resource density, and the probability of working on a particular task, is proportional to the fitness benefit to be had from the task. Another way to express this is that the fitness benefit of a unit of work is the same for all tasks, and tasks only vary in the amount of work that is available to do. This does not seem to be a tenable assumption. Members of a social group encounter resources corresponding to units of work of many different tasks, and assuredly the fitness benefit of a unit of work in one task (for example, feeding one brood item) will be different from another (for example, removing one corpse from the nest). Alternatively, if one defines a unit of work as being that quantity which provides a certain fitness benefit, rather than one 'item' of work in the sense of one worker manipulating one object, it is assumed that the probability of encountering work of a particular type is proportional to the fitness benefit of doing all the available work of that type. This is equally problematic: in some cases it might be true (for instance when there is more dirt on group members, grooming brings more fitness benefit), but in other cases it evidently is not (for example, carbohydrate sources might be extremely abundant, but if the colony's primary present food need is for protein, the fitness value of processing carbohydrate is relatively low).

In short, the problem with the paper is that it makes assumptions under which the fitness benefit of tasks can be directly measured, and sets out a mechanism by which groups can maximise fitness. But the result is a product of the assumptions rather than of the model. The challenge is to understand what effects different tasks have on fitness and how social insects assess which are the most important, an issue which the paper sidesteps with its assumptions.

Notwithstanding its flaws, the work is interesting because it is unique in attempting to relate mechanisms of task allocation directly to fitness effects. Other authors, by contrast, typically show that their model leads to allocation into different tasks with the implication that evolution would tune parameters to give an optimal behaviour within the constraints of the model. The question of what the optimal behaviour actually is, and to what extent the model achieves it, could perhaps be asked more often.

2.3.3 Models applicable to both between- and within-role task allocation

Foraging for work

The "foraging-for-work hypothesis" (FFW) was presented by Tofts & Franks (1992) and Tofts (1993). Its main precept is to see work as represented by 'tokens', or items, that are worked on in successive stages and passed between stages rather like items in a factory production line. Workers are modelled as actively seeking work. As long as they can receive and pass on tokens of work, they remain working at the same stage, but if they do not receive items to work on for some time they will move upstream, or if they cannot find workers to receive items that they have worked on, they will move downstream in the chain of tasks. The effect is that, if there are not enough workers at one stage, workers trying to pass items to that stage will fail and some will move into it, and workers waiting to receive items from that stage will receive too few and also move into it. Thus any imbalances in the allocation of labour are evened out.

If it is assumed that all tasks in the colony are arranged in a linear chain, that workers die at some rate in the task at one end of the chain (i.e. foraging) and that new workers emerge into the task at the other end (e.g. larval feeding), the model produces a weak age-task association similar to that seen in some real ant species (Tofts & Franks, 1992; Tofts, 1993; Sendova-Franks & Franks, 1993).

Tofts & Franks (1992) describe FFW in a way that implies it is intended to explain between-role task allocation, applying to the whole gamut of tasks in the colony from nursing to foraging. It is not certain how fine-grained the allocation can be (whether it is just broadly between one role and the next, or whether it covers finer divisions within roles), and another question is what happens to tasks that cannot be fitted into a linear chain. Whilst a large proportion of the colony's work consists of processing food, and therefore alimentary tasks can form a single chain, there are other tasks which operate on unrelated material: hygiene-related tasks operate on debris, building on nest material (wax, pulp, soil), and so on. Even food items may be processed in parallel chains, typically with proteinaceous sources like pollen or prey being treated differently from carbohydrate sources such as nectar or honeydew. There is no intrinsic reason why two or more such chains could not exist in a colony for handling different items, within each of which FFW might operate, but then some additional mechanism

would be needed to balance the effort expended on each.

Another possibility is that processing of food could provide a primary chain determining role within the colony, and that non-alimentary tasks are done as offshoots or sidelines by workers in each role. For instance, food foragers might also forage for building material, and forage recipients might also carry out removal of nest debris, though the determination of role would be through the pattern of food distribution rather than through the relative demands of building or of nest tidying. Certainly the studies of Blanchard *et al.* (2000) and Cassill & Tschinkel (1999b) suggest that food distribution plays an important part in task allocation in some ant species.

Finally, FFW could be applied to partitioned tasks, where within-role task switching could take place. Partitioned tasks are precisely those where material is passed through several handlers (Jeanne, 1986a; Ratnieks & Anderson, 1999a), and so have the natural structure for FFW. The archetypal example is leaf collection in leaf-cutter ants which involves multiple stages of cutting, collection into caches, and transfer to the nest sometimes via intermediate caches on the way. It is not known how leaf-cutter ants regulate worker numbers in these subtasks, but the work of Jeanne (1986b) (described on p. 23) shows that building in *Polybia occidentalis* contains at least one of the elements of FFW: a worker that fails to pass its token to the next stage may shift to working on that stage itself.

Tofts & Franks (1992) suggest that, while FFW on its own has been proved sufficient to lead to a flexible and well balanced division of labour, in real social insect colonies it could be combined with the influences of other factors such as genetic predispositions or age effects. This makes FFW a little difficult to test since showing a genetic or age effect does not necessarily eliminate FFW. To eliminate FFW, one would have to show that the genetic and/or age effect accounted for all observed variation, but usually such effects are demonstrated by keeping all variables constant except the one under investigation. The result is that one only shows that *in the absence of other factors*, factor x has an effect. To prove that factor x was the principal factor one would have to manipulate it in combination with the other factors, which is far more difficult. Here again, it would be useful to have some predictions from FFW that could be considered 'diagnostic', that is, pecularities of the mechanism that would distinguish it from others. The main prediction actually given is that it leads to a flexible, robust division of labour—but then, so would any other convincing candidate mechanism.

Response thresholds

The notion of stimuli eliciting responses in an organism has been around for most of the past century, and from it leads naturally the idea that those stimuli must exceed some threshold to elicit their response. Whilst the stimulus-response paradigm has been influential in the study of the behaviour of single organisms, its interest to students of social insects springs from the possibility that different members of a social group may have different thresholds for various stimuli. These differences could then lead to a division of labour, if a stimulus is at such a level that some individuals work on the associated task and others do not.

Just as this idea is extremely simple, so it has been proposed that such intrinsic differences between individuals could be the wellspring of the simplest division of labour in primitive social groups (Fewell, 1998). Indeed, since (through both genetic and environmental differences) individuals will never be completely identical in their responses, it is even suggested by Fewell (1998) that some degree of division of labour is actually an inevitable consequence of group living, rather than something which has had to evolve from an undifferentiated state. (Such spontaneous division of labour would, though, still have room to become considerably more adaptive in terms of the relative effort given to different tasks.)

However, the concept of response thresholds is not only simple but extremely powerful, and of all the models mentioned in this thesis, response thresholds occupy the most prominent place in the literature. Their explanatory power is great: they can account for a great many phenomena observed in social insects. Indeed, if there is anything wrong with them, it is that they are capable of too much rather than too little. By being able to account for almost everything, they risk being able to *explain* rather little. They would perhaps be better described as a modelling paradigm than a model, since within the broad definition of response thresholds there is room for an infinity of modelling implementations.

The most exhaustive study of response thresholds has been in two papers by Bonabeau *et al.* (1996) and Bonabeau *et al.* (1998a), the latter extending the findings of the former in several directions. In the first, they introduce their definition of response thresholds and produce some simple findings from the model. Firstly, in the case of one task and inactive or active individuals, they give the probability of an inactive individual taking up the task in a unit of time as being

$$P = \frac{s^2}{s^2 + \theta_2}$$

where s is the level of stimulus for the task, and θ the response threshold. The effect of this is that when s is much less than θ, the probability of performing the task is close to zero, and when s is much greater than zero, the probability of performing it is close to 1. (See Figure 3.1(a) on p. 51 for a sketch of the threshold function.) Active individuals have a constant probability per unit time of becoming inactive. The stimulus intensity increases at a constant rate (due to some accumulating demand for work) and decreases in proportion to the number of individuals active.

For initial studies, the authors divided workers into two castes, one with a high threshold for the task and one with a low threshold, and showed that the amount of work done by the high-threshold caste (those that only perform the task when the stimulus is high) varied with the proportion of that caste in the group in a very similar way to the results of Wilson (1984), who varied the major-minor ratio in several *Pheidole* species (ants with dimorphic workers) and observed the amount of social behaviour in majors. Majors (corresponding to the high-threshold individuals) performed very little work if they constituted less than half of the group, but the amount they performed rose rapidly if they were more numerous. In the model, this is for the very simple reason that, when there are enough minors to do all the work, their activity keeps the stimulus level low, but once the number of minors falls below a critical point, the stimulus level begins rising into the region where majors become activated.

In general, if individuals have varying thresholds, it can be seen, firstly, that those whose thresholds are lower than the current stimulus intensity will do most of the work, and secondly, that if the stimulus is accumulating faster than it is being performed, more individuals will be activated until it equilibrates.

The next step is to consider two tasks. Here, individuals can be inactive or can be active in either task. Transitions between states are as before. An individual becomes active in a task according to the same threshold function, except that the stimulus intensity and the individual's threshold are specific to that task. The transition from active to inactive again occurs with constant probability per unit time. Transition from activity in one task to activity in the other can only occur *via* the inactive state. It is not made

clear how different tasks compete for active individuals.

Two cases are considered: one caste has lower thresholds for both tasks than the other, in which case moderately good agreement is obtained with Wilson's (1984) results on performance of social behaviour and self-grooming by majors and minors, or each caste is 'specialized' in one of the tasks. In this latter case it is predicted that a caste will perform its 'preferred' task (i.e. the one it has a lower threshold for) exclusively when it is in a small minority, but when more numerous will perform the less preferred task more often.

The results described so far relate principally to morphological castes. Most ant species have only one worker caste (Hölldobler & Wilson, 1990), as do all bees and wasps, and in those that do have more than one morphological worker caste, a generalist caste is in the majority, indicating that flexibility remains of great importance (Tofts & Franks, 1992). Bonabeau *et al.* (1996) argue that the results could equally apply to age castes, or "simply groups of individuals with different behaviours," indicating that workers in different roles are being modelled. However, rather than modelling a mechanism to determine how many individuals should be in each role (like the other between-role task allocation models described on pp. 25–26), it shows a way in which imbalances in the number of workers in each role could be responded to in the short term without workers actually changing role (if role is defined by reference to intrinsic thresholds rather than to actual task performance). Nonetheless, workers with a high threshold for a task can only be activated by dint of allowing the stimulus for that task to reach high levels. In other words, under this mechanism a response to under-performance of a task only occurs through the shortfall in task performance being considerable, and only acts to prevent the shortfall becoming greater rather than reducing it to acceptable levels. Thus it should be seen as an adjunct to optimising (preferably dynamically) the numbers in each role rather than as a substitute for it.

A limitation in the way that Bonabeau *et al.* (1996) model response thresholds (rather than an intrinsic limitation in the idea of response thresholds itself) is that stimuli are taken to be global. The authors observe that, "An important question is to understand how this flexibility [in division of labour] is implemented at the level of individual workers, *which certainly do not possess any global representation of the colony's needs*" (emphasis added). Yet that is exactly what they proceed to assume: "This problem can be divided into two parts: (i) how do workers find or gather the information necessary to decide whether or not they switch tasks or engage in task performance;

(ii) how do they actually decide what to do, once they have the information? We shall not address the first question in this paper, and assume that each task is associated with a stimulus... [and] that each insect encounters all stimuli with equal probability within some period of time..." This assumption may be justifiable for an initial exploration on the grounds that it simplifies the modelling considerably, but it does also (as with some models previously discussed) limit its applicability rather severely.

In fact, I would argue that the distinction the authors make is unwise. True, it is useful to separate conceptually the obtaining of information and the taking of decisions based on that information. It is also true, however, that a decision is only as good as the information it is based on. Consequently, a model of decision making will only be as good as its modelling of information. If one has a good model of the workers' decision making rule, but one models the information available to workers too simplistically, one's model as a whole will be too simplistic. In order to understand task allocation in social insects, we must understand both what information is available to workers, and how they act upon it.

The later paper (Bonabeau *et al.*, 1998a) extends the earlier, removing some of its limitations. The first of these additions is a discussion of experimental evidence for response thresholds. There is actually rather little, but this is attributable more to its not having been sought than to response thresholds necessarily being uncommon. At least one of the examples they give illustrates nicely the potential weakness of response thresholds as an explanatory device: Detrain & Pasteels (1991) examined defence in the ant *Pheidole pallidula* and found that majors were recruited to defence only by very large numbers of intruder minor workers, or by a small number of intruder majors. Alien minor workers led to weak recruitment efforts on the colony's majors, to which they did not respond, whereas they did respond to the frantic recruitment efforts made when alien majors were present. This indicates a response threshold in the majors, but the key element to the collective behaviour is not the response thresholds of majors but rather the fact that minors made a greater effort to recruit majors when they encountered alien majors than when they encountered alien minors. Thus the behaviour can be described in terms of response thresholds, but response thresholds in themselves do not really *explain* what is happening.

The other extensions involve ways in which the basic threshold model can be adapted to produce a variety of behaviours. Performance of tasks in sequence is simulated in two ways: by giving workers successively higher thresholds for each task and causing

each to take successively longer to complete, or by having items of one type transform into items of the next when worked upon. The question is then addressed of what happens if encounters with task stimuli depend on what task each worker is currently performing. The probability of encountering task i stimuli (which, along with individual thresholds and global stimulus level for that task, determines task performance) is close to 1 for a worker currently performing task i, and close to zero for a worker currently performing another task. This can produce specialisation as some workers work on one task and consequently are likely to continue encountering it, and others work on the other (two tasks are present) and similarly continue encountering it. It is then shown that temporal polyethism can arise, not by having thresholds change with age (though that presumably would work) but simply by having encounter probabilities depend on worker age. Finally the effect of diversity of thresholds within the colony is explored, showing that preferences of different individuals for different tasks can be present within an overall scheme of progression through three tasks.

Even though temporal polyethism can be achieved simply on the basis of encounter probabilities, rather than by causing thresholds to vary with time, it seems reasonable that in reality temporal polyethism would actually occur through varying thresholds as well as varying encounter probabilities. In either case, it is in some sense true that response thresholds do not themselves explain temporal polyethism; rather, the determining factor is the way that encounter probabilities or response thresholds vary with time, which strictly is beyond what the response threshold model itself can say. Bonabeau *et al.* (1998a) do not really model *how* encounter probabilities change with time, but simply assume that they *do* change with time. Thus there is room for further development of the modelling.

The examples that the authors give from social insect biology are more to do with between-role than within-role task allocation, but in my opinion response thresholds are best suited to explaining how short-term mismatches between task allocation and task demand could be compensated for. Longer-term changes are likely to involve factors that, as I have suggested, fall outside the scope of response thresholds themselves. Because of this ambiguity, and also because of their importance, response thresholds have been placed in this separate section.

The response threshold model has been developed by Theraulaz *et al.* (1998) to include reinforcement: performing a task reduces an individual's threshold for that task. This and other reinforcement-based models are discussed in the Introduction to Chapter 3,

as it is particularly relevant to the work presented there.

A final remark about the response threshold models developed by Bonabeau *et al.* (1998a) is that the paper has perhaps something of the air of being concerned more with showing the diversity of phenomena that the model can produce than with producing predictions that could be used to investigate its accuracy. Whilst it is quite right and necessary to explore a model's possibilities thoroughly, I would like to finish this chapter by reiterating the view that the primary aim of modelling should be falsifiability, at least if the intention is that the model should be an applied model rather than an exploration of the possible. Modelling in the study of social insects is relatively young, and there are already signs (e.g. Camazine *et al.*, in press) that the link between modelling and experimentation is beginning to be held in greater, indeed paramount importance.

Chapter 3

Propensity reinforcement as a task allocation algorithm

3.1 Introduction

3.1.1 Skill refinement, specialisation and task allocation

On the basis that a worker who performs the same task repeatedly is likely to improve her performance, we might expect task allocation mechanisms to be favoured that tend to cause workers to stay in the same task.

One obvious, simple class of rule that individual workers could use which would have such properties is, "Respond to a task stimulus with higher probability if you have been performing that task in the recent past, and with lower probability if you have not." Phrased another way, under such a rule, the more a worker performs a given task, the more likely it becomes to perform it in future, and conversely, the less it performs a given task, the less likely it becomes to perform that task in future.

How reasonable, on available evidence, is the above proposition? If task allocation mechanisms that lead to worker specialisation are to be favoured by selection, not only must repeating the task lead to increased efficiency, but the benefits thereby accrued must be greater when a worker only attempts to achieve heightened efficiency in a

single task. The case that practice improves performance is examined below; first, though, let us consider how it might be advantageous for a worker only to become adept at a single task.

Consider a worker that has so far become skilled at one task. There are two possible costs associated with it taking up a second task. Limits on cognitive capacity may cause it to lose the skills it had acquired in the first task as they are displaced by the second. Whether this occurs will be a characteristic of the species and, perhaps, the tasks. However, whatever the cognitive capacity of the species' workers, there will also always be a 'hidden' cost of switching as the worker uses time learning the new task which otherwise could have been used exploiting its skill at the first task. The magnitude of this cost will depend on the extent to which workers can improve their efficiency at the two tasks and the time it takes to do so, but the cost will always be present to some extent.

3.1.2 Evidence for skill refinement

Do social insect workers actually increase their efficiency at performing a task with practice? For certain tasks, there is evidence that they do. Foraging bumblebees improve their overall performance (Cartar, 1992) by learning to handle particular flower types correctly (Heinrich, 1979; Laverty, 1980) and by learning which flower types are more rewarding (Dukas & Real, 1993; Dukas & Waser, 1994). It has also been shown that learning about novel flowers can impair performance at discriminating between previously learnt flowers (Dukas, 1995), an example of the stronger type of switching cost mentioned above, and the better learning performance of social bumblebees over solitary bees has been attributed to the ability to specialise on a foraging duty (Dukas & Real, 1991).

Similar reasons to those seen in bumblebees cause honeybees to improve their foraging success through experience (Menzel *et al.*, 1974, 1993). They may also be learning in subtler ways, such as learning to decide correctly when it is profitable to switch between flower types or patches. Certainly their performance continues to increase over much of their foraging lifespan (Dukas & Visscher, 1994), suggesting that there are many learning components. Foragers of the eusocial wasp *Polybia occidentalis* have also been shown to improve their performance with experience (O'Donnell & Jeanne, 1992; see also Raveret Richter, 2000, for a general review of eusocial wasp

foraging).

Ant foraging differs from bee and wasp foraging in that, taking place on a surface, pheromones can be used to produce collective strategies in which individual learning may give way to adaptations in the collective pattern (Deneubourg & Goss, 1989). Nonetheless, it has also provided evidence of adaptations by individual foragers (Johnson *et al.*, 1994; Schatz *et al.*, 1994; Fourcassié & Traniello, 1994; Traniello, 1989) which should lead to similar types of performance enhancement to those seen in bee foraging.

Aside from foraging, refinement of task performance has been shown during nest building. The primitively eusocial wasp *Polistes fuscatus* has been shown to increase with experience the speed with which it repairs damage to its nest (Downing, 1992). A second example comes from a fascinating paper by Dobrzański (1971) concerning building in the wood ant species *Formica rufa* and *F. exsecta*. These ants (which use sticks and pine needles to build their nest mounds) to start with have to learn not to stand on the twig they are trying to carry! From this they go on to learn how to react to obstacles, how to sidestep them in the first place, and how to incorporate twigs firmly into the nest so as to form a stable, cohesive grille structure.

Although, disappointingly, these examples are not matched by others involving tasks taking place within the nest (learning of colony odour is well established; for review see e.g. Jaisson, 1987, but this is not a case of skill refinement), the reason seems to be more that such phenomena have not been looked for than that they do not exist. If social insects are capable of drawing benefits from the flexibility that learning confers outside the nest, why should they not profit likewise within the nest? Perhaps the environment inside the nest is less rich and complex than that outside, making a greater proportion of behaviour pre-programmeable. It seems unlikely, nonetheless, that refinement of task performance should have no role at all to play inside the nest, although in the absence of data this possibility cannot be ruled out. Here is an area urgently requiring investigation.

One tantalising piece of indirect evidence in favour of a role for skill refinement within the nest comes from studies on the development of the adult Hymenopteran brain. As one might expect, the extensive learning occurring in honeybee foraging is associated with changes to workers' brains (Coss *et al.*, 1980; Brandon & Coss, 1982; Withers

et al., 1993, 1995; Sigg *et al.*, 1997).[1] It is therefore fascinating to note that Gronenberg *et al.* (1996) found greater post-eclosion growth and morphological development of the brain among workers of *Camponotus floridanus* that remained in the nest but experienced nursing tasks than among workers that remained idle within the nest. This strongly suggests that the neurological changes observed not only resulted from the workers' experience of the within-nest tasks, but reflected behavioural adaptations to it.

3.1.3 Aims and outline of the model

The aims of the modelling work presented in this chapter are straightforward. Firstly, to determine whether a reinforcement rule of the type suggested at the start of this chapter can in fact lead to a division of labour amongst workers. Secondly, by exploring the model's behaviour, to find features which may be used to test for the existence of such an algorithm in social insect colonies. Thirdly, by understanding what the algorithm can and cannot do, to predict in which types of situations its presence might be feasible and in which it can be ruled out altogether.[2] Fourthly, to examine existing data and consider to what extent the behaviours and timescales of the model are compatible with them.

The approach of the model is to describe work as discrete items, of as many types as there are tasks; thus each task does not consist of a global stimulus, but rather of zero or more items scattered across the environment, each representing both a unit of work and a stimulus that elicits the work from a worker. Each worker encounters task items sequentially (it can only encounter one item at a time) and for each task it has a 'propensity', which is the probability that it will work on an item of that task if it encounters one. Reinforcement occurs when a worker works on a task item: its propensity for that task increases, whilst its propensity for other tasks decreases. If a

[1] There is some question as to how much changes in gross morphology (Withers *et al.*, 1993) are *directly* attributable to experience: Withers *et al.* (1995) found that some of the changes in gross morphology were probably immediately due to levels of juvenile hormone (which itself is influenced by colony circumstances under natural conditions; Huang & Robinson, 1999), and were unable to determine whether experience of the external environment played a role in others, but Sigg *et al.* (1997) showed that at least some changes were directly attributable to foraging activity. In concert with results on microscopic changes (Coss *et al.*, 1980; Brandon & Coss, 1982), it seems highly likely that experience has a direct effect.

[2] Although authors who publish models are usually eager to find situations that their model can describe, ruling out the involvement of an apparently reasonable mechanism performs at least as valuable a service.

worker encounters an item but does not work on it, its propensities for all tasks move towards a low resting level. The work presented here is an extended study, with slight modification, of a model originally set out by Spencer *et al.* (1998, reproduced in Appendix B).

3.1.4 Existing reinforcement-based models

Whether explicitly or implicitly, the idea that reinforcement could be a general element in the organisation of social insect colonies appeared as soon as the ideas of self-organisation began to be applied to the study of social insects (Deneubourg, 1977; Prigogine, 1976, pp. 110–115). Self-organisation always involves the generation of structure through a combination of positive and negative feedback in the interactions between many similar subunits; that is, some parts of the system are self-reinforcing, simultaneously inhibiting (directly or indirectly) the development of others (for examples in the social insects see e.g. Deneubourg & Goss, 1989; Bonabeau *et al.*, 1997; Deneubourg *et al.*, 1999; Camazine *et al.*, in press).

For social insects, we can distinguish between those situations (or models) where the reinforcement occurs outside the bodies of workers, as for example pheromone trails in foraging (Franks *et al.*, 1991; Watmough & Edelstein-Keshet, 1995; Edelstein-Keshet *et al.*, 1995; Stickland *et al.*, 1993, 1995, 1999) or nest building (Karsai & Pénzes, 1993; Deneubourg & Franks, 1995; Franks & Deneubourg, 1997; Bonabeau *et al.*, 1998b; O'Toole *et al.*, 1999; Theraulaz *et al.*, 1999), and those where the reinforcement occurs actually within the workers themselves, by the modification of some internal parameter. In the first case, a given worker will always react the same way to a given stimulus, but the system evolves because the stimuli change due to the activity of the workers. In the second case, the stimuli may remain the same, but the response of a worker to a particular stimulus evolves over time according to the worker's experience, and it is this change that drives the evolution[3] of the system as a whole. This change in a worker's reaction to stimuli may be described as learning, since learning is often defined as a long-term change in behaviour dependent upon experience (Alloway, 1972; Matthews & Matthews, 1978). However, it is a much simpler form of learning than the skill refinement discussed above, with which it should not be confused.

[3]The term 'evolution' is used here in the mathematical/physical sense, not the Darwinian.

Two models have used learning of this type to explore somewhat different questions to those addressed here. Deneubourg *et al.* (1987) used a reinforcement mechanism to show how social insect foragers can 'learn' to specialise on profitable foraging areas. Thus the question addressed was primarily how to select between different means of accomplishing the same task, rather than how to decide which task to do. The formulation of the model was consequently different: workers had a probability of leaving the nest to forage, and then a probability of choosing one or the other of two foraging sites; but these probabilities were reinforced by the foraging success at each site; thus multiple sites were offering the same type of item and workers chose between sites, whereas in the model presented in this chapter, workers encounter multiple types of item on a single site and then choose on which type(s) to work. Although the model of Deneubourg *et al.* concentrates on workers choosing between foraging sites, the implications of the paper were much broader as the authors took care to emphasise the potential importance of such reinforcement learning not only in foraging but in the division of labour in general.

Plowright & Plowright (1988) introduce what they describe as "a positive feedback model" for the emergence of elitism. It includes a "job satisfaction" level for each task which increases when the task is performed (and decreases when it is not), and the probability of performing a task is an increasing function both of this and of the level of task stimulus. They show that, depending on the magnitude of increase or decrease, workers may either be all "loafers" (rarely working), or all "elitists" (nearly always working), or they may show a bimodal distribution with some working very frequently and others only rarely. Unfortunately it is not clear from the description of the model how many tasks were present, nor how task encounter probability was determined. Results given show only overall amounts of work done by workers, and do not indicate whether individual "elitists" were true elitists (in the sense I am using), performing all tasks indiscriminately, or specialists, concentrating on a single task.

Closer to the model presented here is that of Theraulaz *et al.* (1998). This is an extension of the fixed threshold model (FTM; Bonabeau *et al.*, 1996, 1998a) (discussed in Chapter 2) to include variable thresholds. It has a similar purpose: to consider whether reinforcement 'learning' can lead to specialisation, and to make predictions about diagnostic features of the algorithm that can be used for empirical tests. The functions used have a somewhat different behaviour (Figure 3.1). Furthermore, the difference in the modelling approach is significant and warrants discussion.

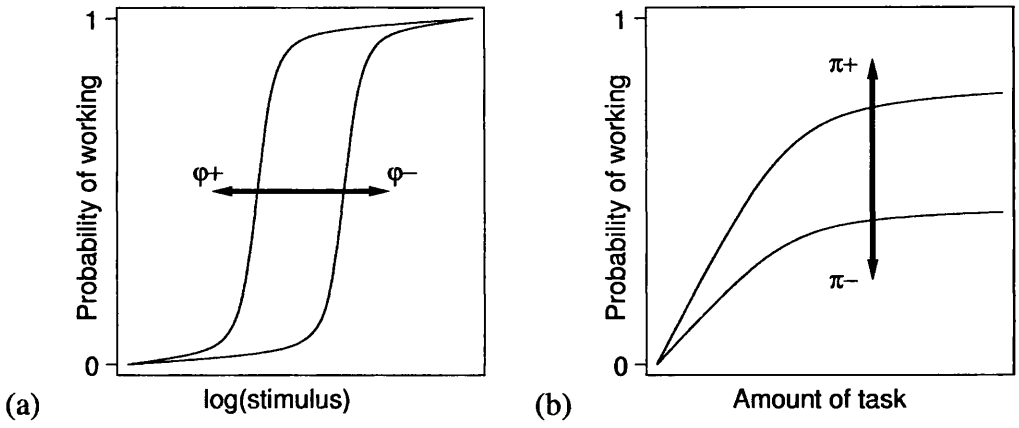


Figure 3.1: Comparison of functions in (a) the threshold reinforcement of Theraulaz *et al.* (1998) with (b) the propensity reinforcement model presented here. The lines on each graph (diagrammatic only) represent the relationship between task abundance and the probability that a worker is working at a given moment; the arrows indicate how these relationships change as the variabless θ and π, respectively, are changed.

In common with its parent, the FTM, the threshold reinforcement model of Theraulaz *et al.* (1998) treats each task as a global stimulus. Rather than simple probabilities of responding to individual task items that can only be encountered or not encountered, workers have thresholds, and the probability of task performance is a sigmoidal function of both the worker's threshold for that task and the current (global) stimulus intensity of the task. Introducing the FTM, Bonabeau *et al.* (1998a) argue: "Two aspects of labour can be discussed: (1) How is information gathered by workers? (2) How are decisions made on the basis of such information? ... [These two aspects] should not be confused in the modeling process... We shall not address the first question in this paper, and assume that each task is associated with a stimulus or set of stimuli."

This distinction may be a convenient one for humans to make, but there is no *a priori* reason to assume that social insects make it: on the contrary, the reception of stimuli and the taking of signals are likely to be closely interwoven (see previous chapter). Theraulaz *et al.* (1998) assume that workers know about the global stimulus levels of all relevant tasks, which is not realistic for most situations. They are also obliged to introduce a stochastic term 'that simulates the fact that individuals encounter slightly different local conditions.' (Presumably specialisation does not otherwise arise.)

A cleaner solution is to make stochasticity an inherent part of the model rather than a bolted-on element, by modelling stochastic encounters between workers and items of work. This also allows the model to be extended without altogether rewriting it,

modelling encounters between workers and items in different ways without changing the way that workers respond to task items (as illustrated by the next chapter). Many task-associated stimuli in social insect colonies are particulate in a way that is better modelled by discrete task items and response probabilities than by global stimuli and thresholds. The threshold approach and the approach used here should be seen as complementary: each is best attuned to only part of the range of task situations found in social insects, and ultimately a way needs to be found of combining the advantages of both.

3.2 Individual behaviour

We can divide the mechanisms of the model into two parts.

1. The model needs rules to determine whether a worker works on each task item that it encounters, and how each of its encounters affects its future behaviour.
2. The model must include a mechanism to determine which task items a worker encounters, and how the behaviour of the worker(s) affects its future encounters.

The model is more easily understood by separating these two elements and examining first the behaviour of a single worker under various predefined task encounter patterns, before considering the behaviour of multiple workers whose encounter patterns are affected by the work that they do. (In other words, we implement the first of the above items and move on to consider the effect of implementing the second.)

3.2.1 Methods

For each task type i, the worker has a 'propensity' π_i which is the probability that the worker, if it encounters a task item of that type, will work on it. When the worker works on an item of task i, its propensity for that task increases, at a rate governed by a 'learning' parameter, λ:

$$\Delta\pi_i = f(\pi_i, 0, 1, \lambda). \tag{3.1}$$

Simultaneously its propensity for any other task(s) j decreases at a rate governed by a 'forgetting' parameter, ϕ:

$$\Delta\pi_j = f(\pi_i, 1, 0, \phi), \quad j \neq i. \tag{3.2}$$

If a worker rejects a task item, i.e. does not work on it, its propensities for all tasks approach a resting level, R, at a rate governed by the forgetting parameter ϕ:

$$\Delta\pi_i = f(\pi_i, 1, R, \phi) \tag{3.3}$$

if $\pi_i > R$, or

$$\Delta\pi_i = f(\pi_i, 0, R, \phi) \tag{3.4}$$

if $\pi_i < R$.

The function used to model changes in propensities is

$$f(x, a, b, q) = \frac{(b-x)(x-a)q}{b-a} + (b-x)q^2 \tag{3.5}$$

which, for $0 \leq a \leq 1$ and $0 \leq b \leq 1$, causes propensities to move across the space between a and b in the direction of b, at a rate that is slow near a and b and faster in the middle of the space, and that is proportional to the parameter q (for which is substituted 'learning', λ, or 'forgetting', ϕ). As long as q is greater than zero and less than approximately 0.618, propensities will remain within the bounds of a and b (see Appendix A). This function was chosen in order that workers that were entrained on doing or on not doing a particular task would not be greatly affected by a small number of encounters with the non-favoured task, but would still respond to a larger number of encounters, thus effectively increasing the element of reinforcement. The form of the function is illustrated in Figure 3.2. The second term in equation 3.5 ensures that $f(x, a, b, q) > 0$ when $x = b$, which is necessary to prevent propensities becoming 'trapped' at extreme values (see figure legend). However, as long as such a feature is present, the exact shape of the function does not affect the dynamics qualitatively.

We now examine the behaviour of a single worker under these rules in a two-task regime.

The parameters affecting the worker's response to task items encountered are its 'learning' and 'forgetting' parameters λ and ϕ, the resting level R that propensities move towards when task items are rejected, and the initial conditions, i.e. the starting values of the worker's propensities.

Single worker behaviour is initially studied by taking the value of 0.2 for the last two of these as a reasonable starting point, whilst varying the 'learning' and 'forgetting'

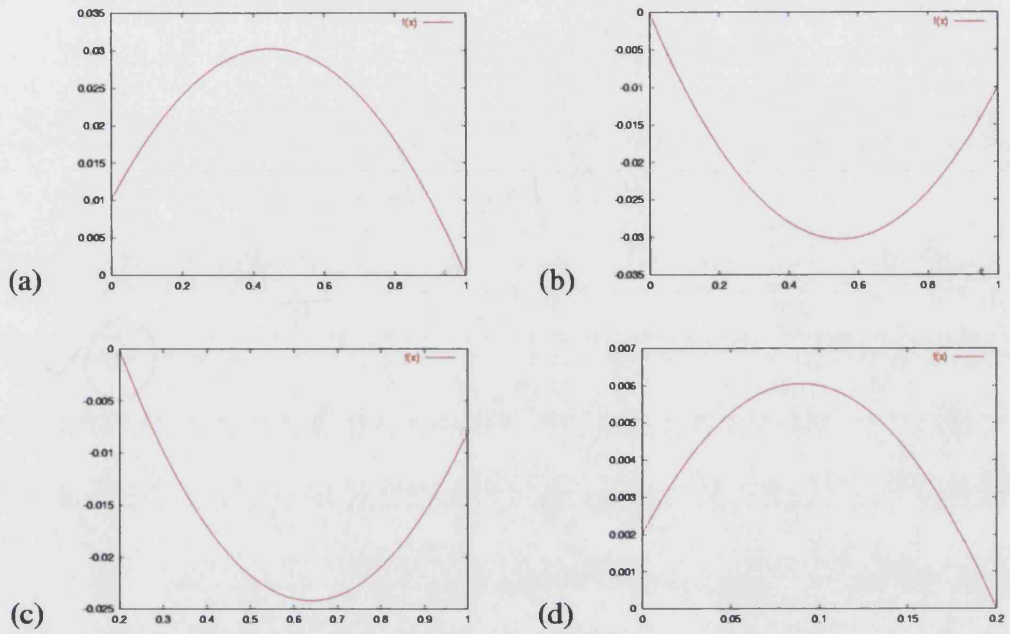


Figure 3.2: Examples of the learning and forgetting function $f(x, a, b, q)$.
(a) $a = 0$, $b = 1$ as in equation 3.1; note that its value is greater than zero at $x = 1$, which is necessary so that learning can occur for a task whose propensity is zero.
(b) $a = 1$, $b = 0$ as in equation 3.2.
(c) $a = 1$, $b = R = 0.2$ as in equation 3.3; note that its value is less than zero at $x = R = 0.2$, which is necessary so that a propensity of 1 can approach R.
(d) $a = 0$, $b = R = 0.2$ as in equation 3.4.
In all cases $q = 0.1$. If $f(x, a, b, q)$ were zero at $x = 0$ in (a) or at $x = 1$ in (c), propensities could become 'trapped' at 0 or 1 respectively.

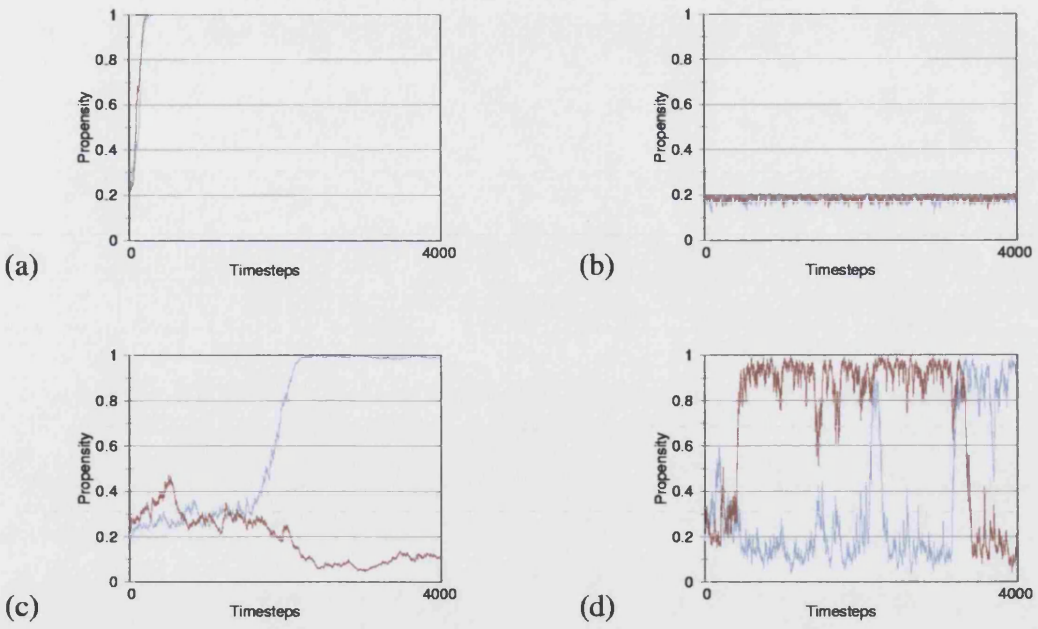


Figure 3.3: Examples of individual behaviour: evolution of the propensities of a single worker presented with a random sequence of work items of two types each with equal probability. $R = 0.2$, starting propensities for both types $= 0.2$.
(a) Elitism—items of both types are almost always accepted; $\lambda = 0.1$, $\phi = 0.01$.
(b) Indolence—items of either type are usually rejected; $\lambda = 0.01$, $\phi = 0.1$.
(c) Stable specialisation; $\lambda = 0.05$, $\phi = 0.018$.
(d) Unstable specialisation; $\lambda = 0.18$, $\phi = 0.09$.

parameters and taking statistics that summarise relevant aspects of the behaviour. The study is then extended by exploring the effect of different values of R and different initial propensities.

3.2.2 Results: effects of 'learning' and 'forgetting' parameters

In this section, we keep R at 0.2 and always use an initial value for propensities for all tasks of 0.2.

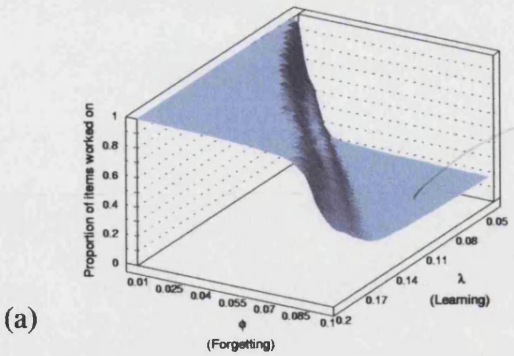
Random task encounters

A worker that encounters task items of two types at random with equal probability (0.5 for each type) can exhibit three classes of behaviour, which can be described as elitism, indolence, and specialisation. If λ is high and ϕ low, propensities for both tasks will increase and level out just below 1 (e.g. Figure 3.3a). If ϕ is low and λ high, propensities for both tasks will remain around R (e.g. Figure 3.3b). With intermediate values of λ and ϕ, specialisation of varying degrees of stability may occur (e.g. Figures 3.3c, d).

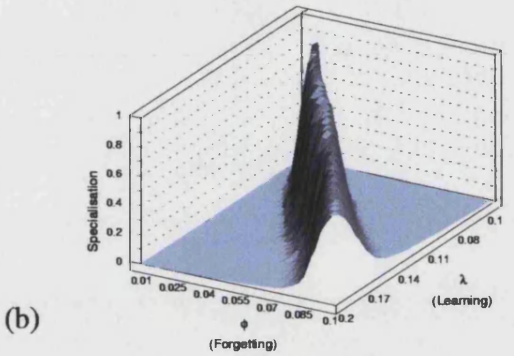
Looking across a range of λ and ϕ space shows that the specialisation behaviour occurs in a band approximately from high λ/high ϕ to low λ/low ϕ (Figure 3.4b), with elitism on one side of the band and indolence on the other (Figure 3.4a). Confirming the existence of task constancy in specialists, Figure 3.4(c) shows that the rate of switching between tasks is lowest in a band corresponding to the zone of specialisation.

Response to new task

How responsive to change is a worker in these various zones of parameter space? The simplest way to measure responsiveness is to allow the model to stabilise with a single task, and then introduce a second. Figure 3.5 shows the results of this. Naturally, a worker in the zone of indolence never responds to the introduction of a new task, as it would not have responded had the task initially been present. In the zone of elitism, response to the new task is relatively rapid, but in the specialisation zone it is extremely slow. This can easily be explained in the light of the results shown in Figure 3.4: elitism in those results means that the worker accepted both tasks and could not maintain a specialisation on only one, a fact that applies whether the second task is present from the start or not; specialisation, on the other hand, implies that the worker can maintain a specialisation on a single task even when it is encountering equal numbers of both, and so it is not surprising that when we effectively induce specialisation by supplying a single task for some time, the worker continues that specialisation when it begins to encounter equal numbers of both tasks. The fact that there is an eventual response in the specialisation zone is attributable to specialisation not being absolutely stable under two tasks, especially with larger values of λ and ϕ (note how, in Figure 3.4(c), switching is slightly greater at the end of the specialisation zone associated with high



(a)



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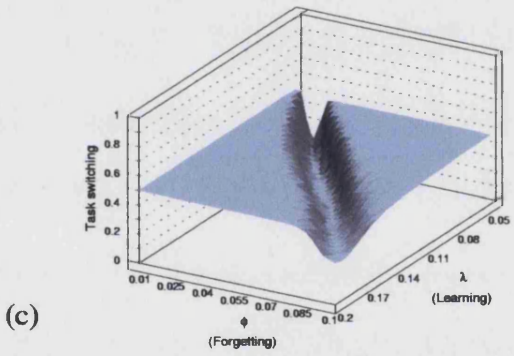


(c)

Figure 3.4: Summary statistics drawn across parameter space $\lambda = 0.05$ to 0.2 and $\phi = 0.01$ to 0.1 for a single worker encountering items of two task types at random with equal probability. $R = 0.2$, starting propensity for both tasks = 0.2.

(a) Work rate: the proportion of task items encountered that are worked on.

(b) Specialisation: $|\pi_1 - \pi_2|$, the absolute difference between propensities for each task. If propensities are the same, the worker is not differentiating between tasks.

(c) Switching: the proportion of items worked on that are of a different type to the previous item worked on.

(Values obtained by running the model 4000 timesteps to allow stabilisation then taking mean values over the following 4000 timesteps; values shown are averages of 100 such runs.)

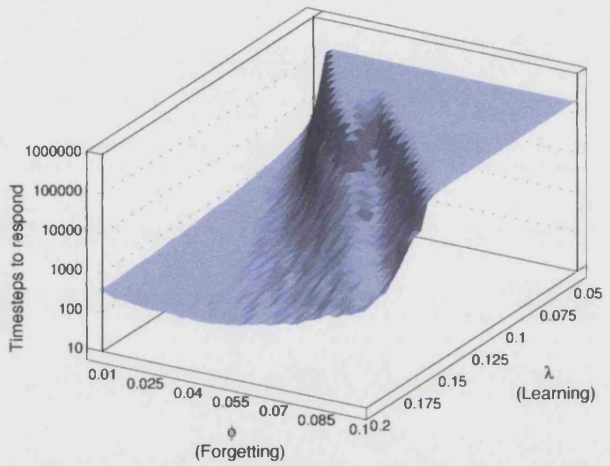


Figure 3.5: Summary statistic across parameter space $\lambda = 0.05$ to 0.2 and $\phi = 0.01$ to 0.1: time taken by a single worker to respond to a new task. The worker encountered items of only one task type for 4000 timesteps, and then encountered items of two types at random with equal probability. The z axis gives the number of timesteps between introduction of the new task and the first occasion on which the worker's propensity for the new task exceeds 0.5 for a period of at least 500 timesteps. Values shown are averages from 20 runs of the model. Runs were stopped 200000 timesteps after introducing the new task; this limit was imposed by availability of computation time but can be considered to be beyond biologically meaningful time scales (it represents 46 days if a timestep is taken as 20 seconds).

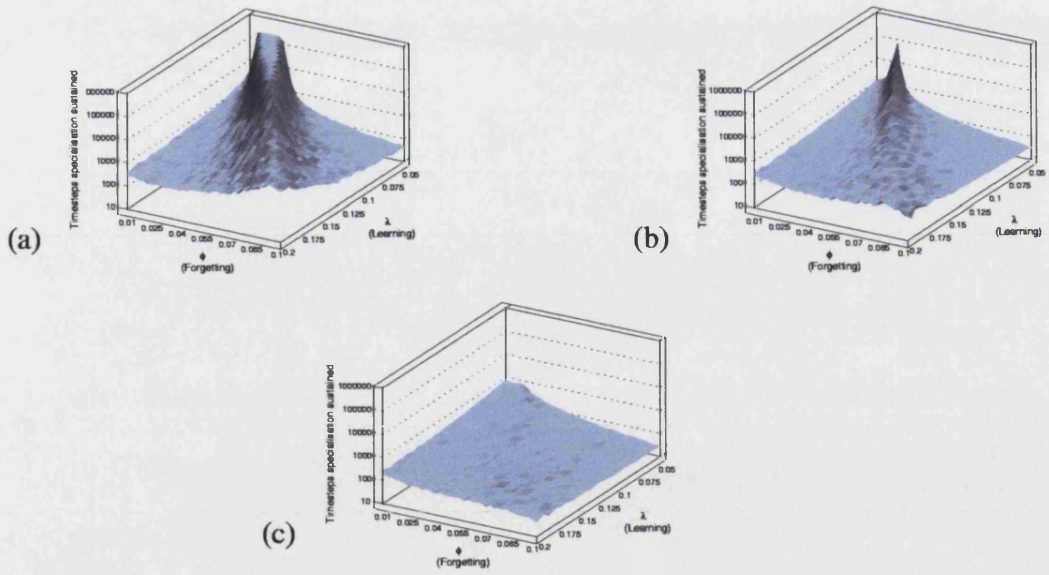


Figure 3.6: Summary statistic across parameter space $\lambda = 0.05$ to 0.2 and $\phi = 0.01$ to 0.1: time for which a worker maintains specialisation on task 1. $\pi_{1(t=0)} = 1$, $\pi_{2(t=0)} = 0$, $R = 0.2$. Time taken for π_1 to fall below 0.8.

(a) Encounter probabilities of 0.5 for task 1 and 0.5 for task 2.

(b) Encounter probabilities of 0.4 for task 1 and 0.6 for task 2.

(c) Encounter probabilities of 0.3 for task 1 and 0.7 for task 2.

The model was not run beyond 200000 timesteps even if specialisation on task 1 was sustained: see legend to Figure 3.5. Values shown are averages from 20 runs.

λ and ϕ, and how this corresponds to responsiveness within the specialisation zone being quicker at the same end).

Unequal task encounters

There may well exist many occasions where workers encounter items of two tasks more-or-less at random. Less realistic is to assume that the probability of encountering the two types should be exactly equal. What happens if this probability shifts slightly? For Figure 3.6, a worker was created as a specialist in task 1 and then exposed to varying encounter probabilities of tasks 1 and 2, and the average time for which it remained a specialist in task 1 was measured. These results indicate that, although the 'unstable specialists' will switch within a few thousand timesteps even when the mixture is equal, the 'stable specialists' will remain so for an indefinitely long time. However, as task 2 forms a greater proportion of encounters, even in the zone of stable

specialisation a worker does not remain a task 1 specialist indefinitely. When the encounter probability for task 1 is as low as 0.3, specialisation on task 1 is sustained on average for under 1000 timesteps even with the lowest λ and ϕ parameters.

3.2.3 Results: effects of R and starting propensities

Put simply, the effect on an individual of increasing R is to decrease the degree of specialisation (when it occurs) and to increase responsiveness.

The graphs shown in Figure 3.7 were produced in the same way as those in Figures 3.4 and 3.5, the only exception being that R, instead of being 0.2, was set to 0.1 in Figure 3.7 (a), (b) and (c) and to 0.4 in Figure 3.7 (d), (e) and (f). Reducing R below 0.2 has little effect on the degree of specialisation, but markedly increases response times to change in task demand. Increasing R to 0.4, however, decreases specialisation significantly, whilst producing an enormous decrease in response times for most combinations of λ and ϕ.

Initial values of the worker's propensities for the two tasks seem to have relatively little importance. If the worker is given initial propensities of 1 for one task and zero for the other (i.e. it begins as a specialist), then in the zones of indolence and elitism (within the λ–ϕ parameter space) it quickly reverts to indolence and elitism, respectively. The only exception is that the zone in which specialisation occurs remains marginally broader for several thousand succeeding timesteps (results not shown).

If the worker is begun as an elitist (starting with a propensity of 1 for both tasks) it remains, of course, an elitist in the zone (within λ–ϕ space) of elitism previously seen; and in the zone of indolence it quickly reverts to indolence. However, in the zone in which specialisation would have occurred had it started with low propensities for both tasks, it is able to sustain elitism for time periods similar in magnitude to the response times shown in Figure 3.5: a few hundred timesteps or less with the highest λ and ϕ values to tens or hundreds of thousands with the lowest.

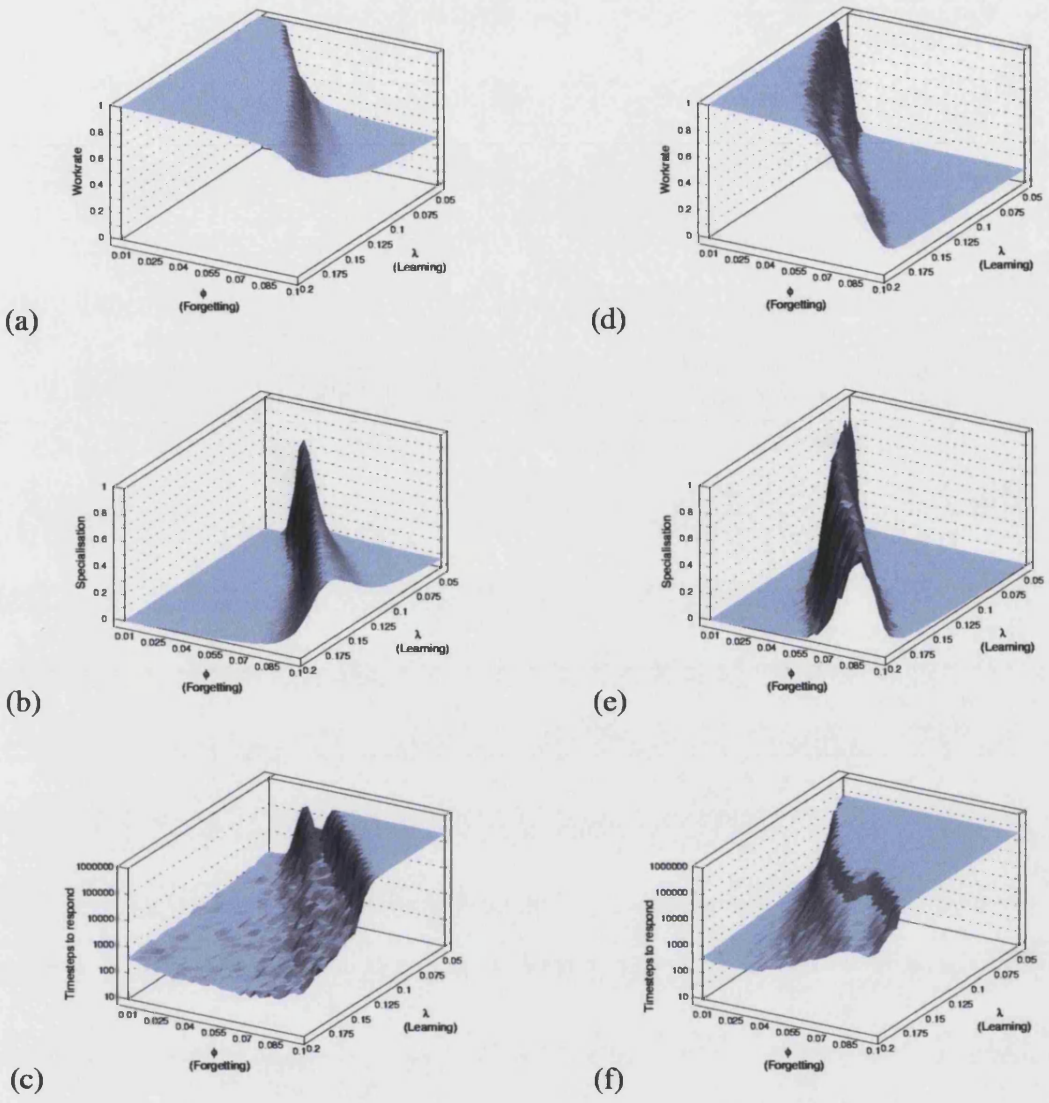


Figure 3.7: Summary statistics drawn across parameter space $\lambda = 0.05$ to 0.2 and $\phi = 0.01$ to 0.1 for a single worker encountering items of two task types at random with equal probability.

Low *R*:

(a) Workrate: as Figure 3.4(a) except that $R = 0.1$.

(b) Specialisation: as Figure 3.4(b) except that $R = 0.1$.

(c) Responsiveness: as Figure 3.5 except that $R = 0.1$.

High *R*:

(d) Workrate: as Figure 3.4(a) except that $R = 0.4$.

(e) Specialisation: as Figure 3.4(b) except that $R = 0.4$.

(f) Responsiveness: as Figure 3.5 except that $R = 0.4$.

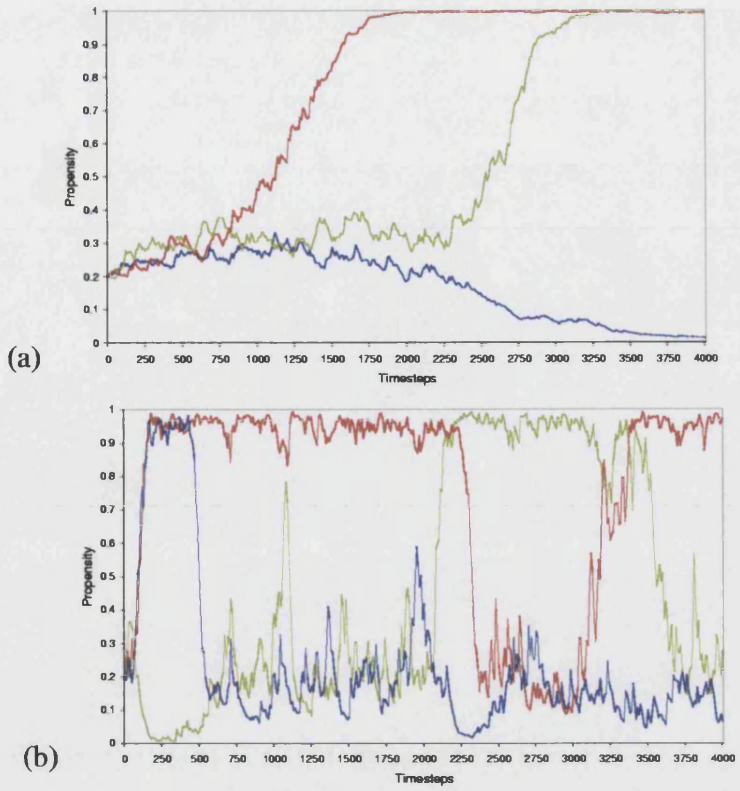


Figure 3.8: Examples of individual behaviour with three tasks: evolution of the propensities of a single worker presented with a random sequence of work items of three types each with equal probability. $R = 0.2$, starting propensities for both types $= 0.2$.
(a) Stable 'specialisation' on two tasks of three; $\lambda = 0.05$, $\phi = 0.01$.
(b) Unstable specialisation; $\lambda = 0.2$, $\phi = 0.06$.

3.2.4 Results: three tasks

When three tasks are present, specialisation does not always occur in the same way as with two tasks. With high values of λ and ϕ, the zone of unstable specialisation under two tasks, a similar picture is observed (Figure 3.8b), but in the zone of stable specialisation, whilst an initial specialisation may emerge on one of the three tasks, it does not last and is succeeded by a 'specialisation' on two of the tasks, rejecting only one (e.g. Figure 3.8a). This specialisation on two tasks out of three appears to be stable once established.

3.2.5 Discussion of individual behaviour

Given random encounters with items of different tasks, the mechanism proposed here can lead to specialisation for some values of λ, ϕ and R.

Why does specialisation occur in a band across the parameter space of λ and ϕ? The way that propensities evolve can be seen as a competition between their tendency to increase when the corresponding task is performed, and their tendency to decrease when other tasks are performed or when task items are rejected. If these tendencies are balanced, even a small difference between the propensities for the two tasks will be amplified as that with the higher propensity is performed more often, depressing further the propensity for the other. If forgetting is too strong, propensities for both tasks will remain low, and being low, items of both types will often be rejected when encountered, so that the propensity for both stays close to R. If forgetting is too weak, then when one task is performed the propensity for the other will not be depressed enough to compensate for the increases it experiences when it *is* performed, and both tasks will be reinforced alike leading to elitism.

The zone in which specialisation can be sustained is congruent with that in which it can emerge from indolence, so starting conditions are not too important unless workers begin as elitists—an unlikely prospect if there are indeed advantages to specialisation.

Different types of specialisation may be seen according to whether the values of λ and ϕ are suitably balanced and large, or balanced and small. When large, an unstable form of specialisation is seen, with occasional switching of the favoured task (every 1000–2000 timesteps for the largest values explored). When small, specialists remain faithful to the same task indefinitely.

In the zone of stable specialisation, however, a worker is necessarily unresponsive if, having become entrained on a single task, a second is introduced accounting for 50% of encounters. By contrast, in the zone of unstable specialisation, a worker does respond to this situation within a biologically reasonable timescale (a few hundred timesteps or less).

Thus there is a trade-off. It is to be presumed that stable specialisation is desirable when conditions are stable, as is an ability to respond to change. A worker can be a stable specialist, avoiding switching tasks unnecessarily when conditions remain sta-

ble, but then it is poor at responding to new opportunities (which is not problematic in a single worker, but must be avoided if all workers behave the same way). Or it can be the reverse: quick to respond but unable to maintain stability. It cannot combine both positive features. To some extent a better compromise between the two can be had by increasing R, but this comes at the expense of reducing the amount of specialisation that does occur within the specialisation zone.

However, as yet we have only supplied a singler worker with items of work according to fixed and predefined probabilities. In reality, the work that a worker does will affect its future encounter probabilities as well as those of its cow-orkers. The next step is to examine an example of group behaviour, making at first the simplest assumptions about the distribution of work.

3.3 Group behaviour

3.3.1 Methods

To model the behaviour of a group of workers each having the properties described in the previous section, the simplest assumption to make is that task items are randomly positioned within some fixed area and that the probability of encountering an item is an increasing function of the numbers of that type of item that are present. We take encounter probability P_i for items of type i to be

$$P_i = \frac{T_i}{T_{\text{total}} + \alpha N} \tag{3.6}$$

where T_i is the number of items of type i available to be worked on, T_{total} is the total number of items of all types, N is the number of workers, and α is a parameter related to the size of the area which is set to 10 for the results given below.

The function gives encounter probability approximately proportional to T_i when $T_i \ll N\alpha$ but approaches $P_i = T_i/T_{\text{total}}$ when $T_i \gg N\alpha$. This represents the idea that each item occupies, or can be detected from within, some fixed area, but that items may overlap at high densities. (For example, one larva may correspond to several 'feed larva' task items, if it remains hungry after being fed a single time. Larvae are not necessarily fed to satiation: in *Solenopsis invicta*, Cassill & Tschinkel, 1995, 1999a, found that liquid food was provided in 'packets' of fixed size.)

Task items accumulate at a fixed rate w_i per task per timestep:

$$T_{i(t+1)} = T_{i(t)} + w_i \,. \tag{3.7}$$

It will be seen that increasing encounter probability as a function of task density causes the system to self-regulate. Workers do not encounter an item every timestep when few items are present; if task performance rate is less than the rate at which new items accumulate, item encounters become more frequent. Neglecting changes in propensities, this causes a proportionate increase in task performance, until an equilibrium is

reached when work is encountered often enough that it is performed at the same rate as it accumulates (unless fewer than w/N of items encountered are worked on).

3.3.2 Results: effects of 'learning' and 'forgetting' parameters and R

When examining single worker behaviour, a statistic used for summarising behaviour was 'workrate', i.e. the proportion of items encountered that were worked on. This was a useful value as long as an item was encountered every timestep.

Now that groups of workers are being modelled, item encounter probability will be variable and less than 1, so that a group that works on a small proportion of items encountered but has frequent encounters may process items at the same rate as a group that encounters items rarely but works on nearly all items encountered. That is the corollary of the equilibrating effect mentioned above and demonstrated below.

What we are interested in, instead, is whether equilibrium between item supply and work rate is reached at a high or low density of items, and consequently whether, on average, items are worked on promptly. The relevance of this question to biological fitness is clear since, for example, if larvae are left too long unfed they may die and will certainly grow less rapidly than otherwise, or if colony debris equilibrates at a high level the risk from parasites and pathogens will be greater. Therefore, task item half-life (that is, median item age at a given timestep) is used instead of 'workrate' as a measure for studying group behaviour in the model.

Graphs of task item half-life and of specialisation (Figure 3.10a, b) show the same picture as the results from individual workers: a zone of elitism, where virtually all items encountered are worked on, keeping levels low, a zone of specialisation, and a zone of indolence, where most items encountered are not worked on and task items are abundant. The principal difference is in responsiveness to addition of a new task (Figure 3.10c). Here, specialists become much more responsive, due to the equilibrating effect mentioned above: because the new task is initially neglected, it rapidly builds up to higher levels than the pre-existing task, and once it accounts for more than half of task encounters many specialists in the other task begin to switch to it. This can be seen from the evolution of token numbers given in Figure 3.9. The effect is to bring

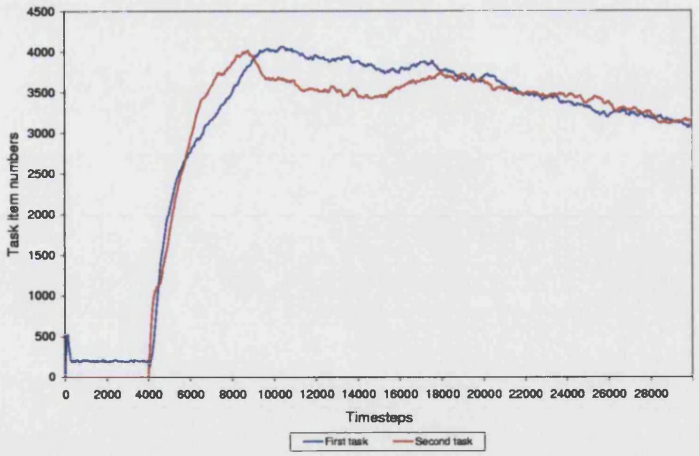


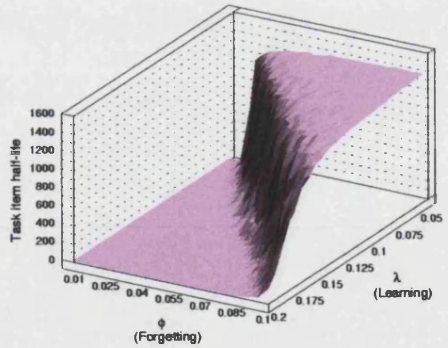
Figure 3.9: Evolution of task abundance when a second task is introduced after entrainment on the first. A second task was introduced after 4000 timesteps. Note how it soon becomes more abundant than the first; there is then an 'overshoot' as the first becomes more abundant again, followed by a gradual equilibration. $N = 20$, $\lambda = 0.1$, $\phi = 0.05$, $R = 0.2$. $w_1 = 10$ and $w_2 = 0$ for $t \leq 4000$; $w_1 = w_2 = 5$ for $t > 4000$.

the response time down to tens or hundreds of timesteps instead of tens or hundreds of thousands of timesteps.

When different values of R are used (Figure 3.11), the relation of group properties to the individual-worker results given above is similar, with quicker responsiveness from specialists being the chief difference.

If one task accumulates at a greater rate than the other, both equilibrate at approximately the same level, as Figure 3.12 shows. Consequently, items of the task that accumulates more slowly will tend to wait much longer to be performed. At the end of the run illustrated therein, there were 19 specialists on the more rapidly accumulating task and 1 on the other.

(a)



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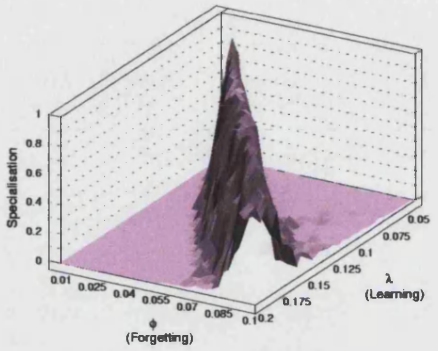

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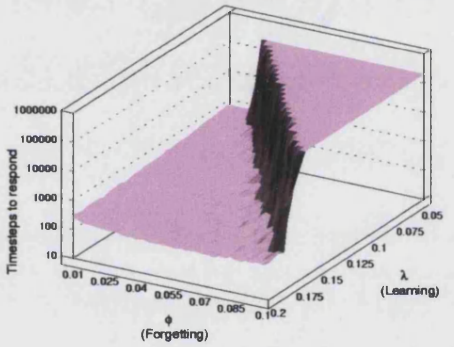


Figure 3.10: Summary statistics drawn across parameter space $\lambda = 0.05$ to 0.2 and $\phi = 0.01$ to 0.1 for workers encountering items of two task types (see text for details of encounter probabilities). $R = 0.2$, initial propensity of all workers for both tasks 0.2, $N = 20$, $w_i = 5$ except that $w_2 = 0$ in (c) when $t \leq 4000$.

(a) Task item half-life: the simulation was run for 4000 timesteps with two tasks, and median item age was calculated.

(b) Specialisation: the simulation was run for 4000 timesteps with two tasks, and the mean specialisation per worker $\frac{\left(\sum_{j=1}^{N} |\pi_{1j} - \pi_{2j}|\right)}{N}$, π_{ij} being the propensity of worker j for task i, was calculated.

(c) Responsiveness: the simulation was run for 4000 timesteps with a single task before adding a second; values shown are the number of timesteps before mean propensity for the new task exceeds 0.5 for a period of at least 500 timesteps. Runs were stopped after 200000 timesteps even if this criterion was not reached; see legend to Figure 3.5.

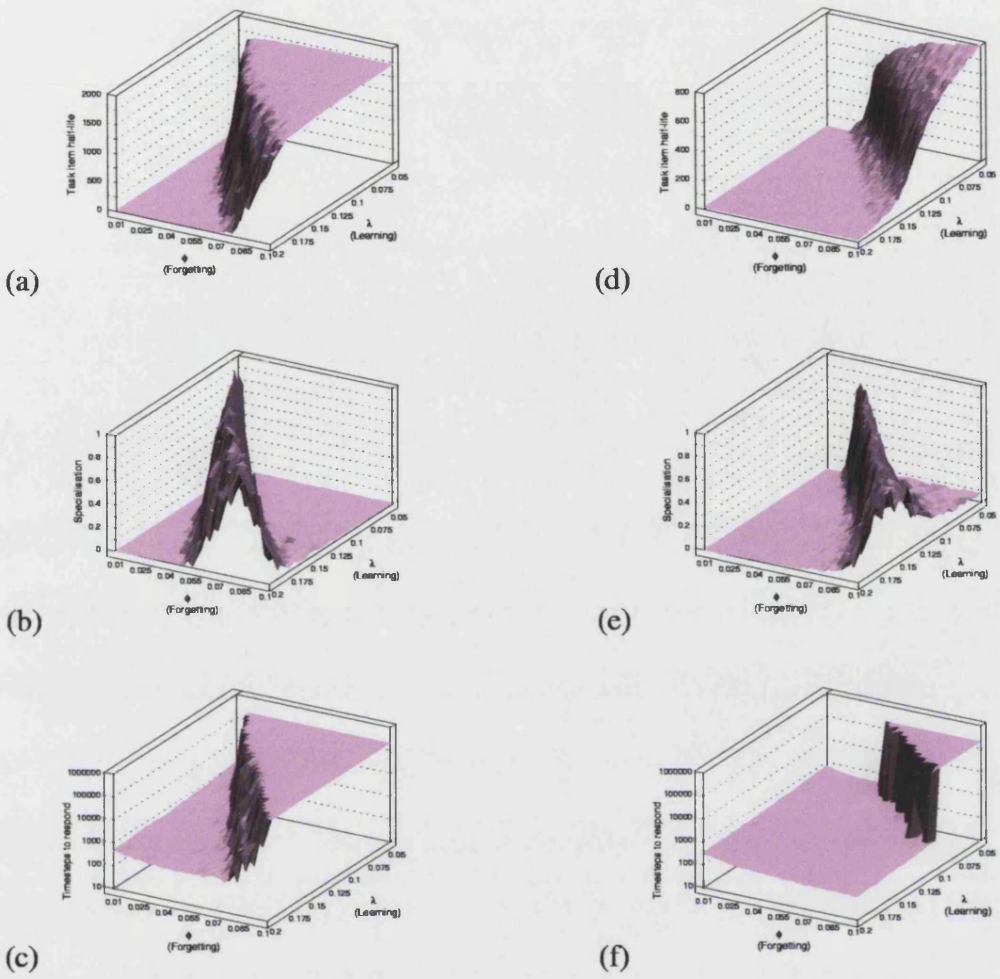


Figure 3.11: Summary statistics drawn across parameter space $\lambda = 0.05$ to 0.2 and $\phi = 0.01$ to 0.1 for 20 workers encountering items of two task types (see text for details of encounter probabilities). Initial propensity of all workers for both tasks 0.2, $w_i = 5$ except that $w_2 = 0$ in (c) and (f) when $t \leq 4000$.

Low *R*:

(a), (b), (c): Item half-life, specialisation, and responsiveness, with $R = 0.1$. As Figure 3.10 (a), (b) and (c) respectively except that $R = 0.1$.

High *R*:

(d), (e), (f): Item half-life, specialisation, and responsiveness, with $R = 0.4$. As Figure 3.10 (a), (b) and (c) respectively except that $R = 0.4$.

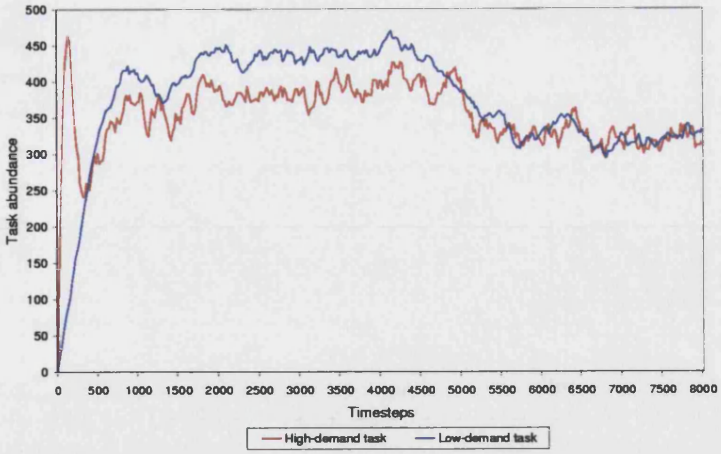


Figure 3.12: Evolution of task abundance when one task is rarer than the other. Both tasks were present from the start. Although the accumulation rate for one is many times the other, both equilibrate at a similar level. $N = 20$, $\lambda = 0.1$, $\phi = 0.05$, $R = 0.2$. $w_1 = 9$, $w_2 = 1$.

3.4 Discussion

3.4.1 Essence of the results

The results presented in this chapter show that the mechanism used of reinforcement of propensities can lead to a division of labour among workers, with some workers specialising on one task and some on another. They also show some limitations to the conditions under which specialisation occurs. In essence, when task encounters are random and encounter probabilities reflect task abundance, specialists will only arise and be maintained for a task that accounts for around half or upwards of encounters. The model does not behave entirely the same way with two tasks as it does with more than two: this is a caution against the common practice of regarding a two-task model as a sensible stand-in for N-task models, and indeed one wonders how many other models would reveal similar effects if applied to more than two tasks. The other principal limitation is that the way the system operates is unfavourable to rare tasks, as these have to reach a relatively high level before performance rate balances accumulation rate.

Under such an encounter rule, the system is strongly homeostatic with task abundance equilibrating at a constant level (aside from short-term stochastic fluctuations) if task items accumulate at a constant rate. The exception is when task accumulation

is faster than the rate at which workers deal with items when encounter probabilities approach 1.

3.4.2 Applicability of the model

The model as developed so far could be applicable to some within-nest activity: task allocation within a role, for example, where the role only comprises two or three tasks (it is assumed that tasks unrelated to the role would not be perceived as stimuli). Encounters with nestmates might approximate randomness, so that grooming or trophallaxis stimuli could be encountered randomly, and even brood might be encountered near-randomly (despite not being randomly arranged; Franks & Sendova-Franks, 1992) if worker trajectories are haphazard enough. Evidence supporting or refuting the types of patterns seen in Figure 3.3 is lacking, however. This is an important gap in empirical studies of social insect task allocation.

Foraging tasks are also likely to present random or near-random encounters with a small number of differentiated types, and here evidence does exist for features such as density-dependent specialisation and switching. The individual foragers of 'generalist' bumble bee species are known to specialise on flower types (Heinrich, 1979; Dukas & Real, 1993), and can respond by switching, after a period, when the preferred flower type is removed (Heinrich, 1979). A case matching even more closely the conditions modelled is that of seed harvester ants: Rissing (1981) offered patches of randomly scattered seeds of novel species, and published graphs of the evolution of individual seed preferences. Preference was measured as seeds harvested as a proportion of encounters, which makes it identical to the propensities used in the model. The graphs of seed preferences bear a striking similarity to the evolution of individual propensities in the model, especially when λ and ϕ are large (Figure 3.3d). This does not of course mean that the mechanism is the same, but the experimental system would be a perfect one for testing some of the predictions made below.

Note that, as the seed-harvester example illustrates, since a propensity is simply the probability of performing some act, we can measure it empirically (provided we can establish when encounters with task stimuli have occurred). A propensity *is* the observed behaviour, in contrast with the idea of a threshold, which is something that can never directly be measured, but can only be inferred from observed behaviour.

We must take care to avoid the trap of believing, because worker i performs behaviour j on six out of ten occasions, that it really did have a 0.6 probability of performing the task on each of those occasions. Behaviours in social insects (and other organisms) are context-dependent (Blanchard, 1997; Rayner, 1997), and there may have been differences of context between the observed occasions of which we were unaware.

Nevertheless, it seems that much social insect behaviour genuinely is probabilistic (Deneubourg *et al.*, 1983), and this direct coupling between the model's chief variable and observable behaviour is a satisfying feature when it comes to verifying the model. To that end, some possible empirical tests for distinguishing features of the model are now suggested. Whilst none, individually, should be seen as definitive, all together should give a strong indication that the mechanism of the model, or something very like it, is in operation.

3.4.3 Suggested diagnostic tests

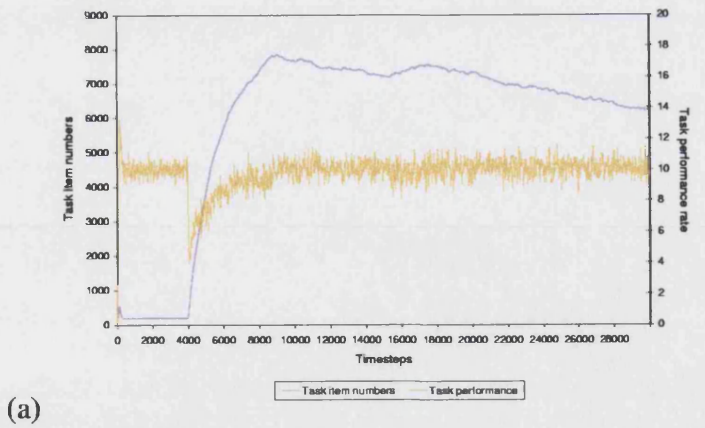
The principal predictions that can be made from the model are as follows. They apply to workers that have λ, ϕ and R values that led to specialisation in the results presented above. I am not assuming that specialisation will always be advantageous, but rather that, if elitism or indolence were the most advantageous behaviour, these would arise by simpler mechanisms (e.g. a rule 'work on everything you encounter' or 'work on almost nothing you encounter'), and therefore that tests for their occurring through a propensity reinforcement effect would not be of interest.

1. When a new task appears, there is

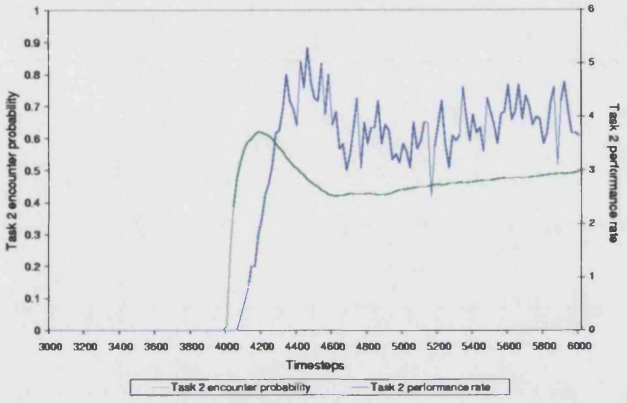
   (a) a decrease in overall task performance (Figure 3.13a), and

   (b) a time lag before the new task is taken up (Figure 3.13b).

   The time lag is not simply that due to the time taken for task items to accumulate: it occurs after encounters with the second task become frequent, because workers are specialising in existing task(s) and consequently have propensities of zero for the new one. Initially, they will reject the new task, causing their propensities to move towards R (hence the drop in overall performance rate). This in turn will cause the new task occasionally to be performed, and its performance will be reinforced by an increasing propensity. If the time lag is very short, specialists



(a)



(b)

Figure 3.13: (a) Evolution of task abundance and task performance, and (b) probability of encountering second task and performance of second task, when the model is run with a single task and a second is introduced (at $t = 4000$). Details as for Figure 3.9 (the graphs are from the same data). Graph (b) shows only the portion of interest around $t = 4000$. Note in (a) the drop in task performance rate when the new task is introduced, even though task abundance is as great, and in (b) the time lag between introduction of the new task and performance of it.

will be found to be unstable (when conditions are stable); otherwise they will show stable specialisation.

2. If stimuli for one task are removed and returned after a brief pause, the same workers that specialised on it before its removal will take it up again, but if the pause is longer, the workers that take it up again will be a random selection from the available pool.

Of course, testing these predictions requires an ability to manipulate abundance of task stimuli, which is easy with some foraging tasks but less so within the nest, and a challenge for verifying predictions of this and any other model of task allocation will

be to find ways of manipulating task levels without causing gross disturbance to the nest environment (see Chapter 7).

3.4.4 Differences between foraging and within-nest tasks

As Spencer *et al.* (1998) pointed out, the model has implications for foraging generally and not just for social insect foragers: many non-social foragers experience similar random distributions of a few different prey types. There are, however, two crucial features that distinguish foraging (by social or non-social organisms) and the inside of the nest in social insects. In foraging, it is not important to pay equal attention to the different prey types (unless diet breadth has to be maintained), but rather to maximise energy harvested against energy or time expended. In the nest, all tasks have to be given attention, and a task cannot necessarily be neglected simply because it is less numerous or inconveniently distributed. Secondly, whilst a foraging organism has to make the best of the distribution of resources that is available to it, within the nest social insects have the opportunity to control the environment and therefore the localisation and distribution of task stimuli.

For instance, they can clump together items of the same task. This could increase the potential of the mechanism studied here to lead to specialisation, by causing individual workers to encounter the same type of item more frequently within a clump. It would also improve efficiency by reducing search time. Notice how, in Figure 3.9, task items equilibrate at a much higher level when two tasks are present than when only one is present ($t < 4000$), even though the overall rate of accumulation is the same. The reason is that when there are two tasks equally abundant, specialists in either spend half their time encountering items that they do not work on.[4] It is, incidentally, rather questionable to use the expression 'search time' when one does not know what the organism is searching for. More neutrally, we might say that giving task items spatial structure could reduce the proportion of items rejected whilst still maintaining specialisation among workers.

Besides these beneficial aspects, spatial arrangement of tasks might reduce respon-

[4]This cost is exaggerated because the model assumes, unrealistically, that rejecting an item takes as long as performing it. Nonetheless, allowing rejection of items to take less time would not affect the results given, since these depend on the *sequence* of items encountered by individual workers, which would not substantively be altered by such a change.

siveness, since by letting workers continue working successfully in a patch of one task type it isolates them from conditions elsewhere. Other, perhaps more urgent tasks may have arisen whilst a worker is occupied within the zone of its favoured task. Is it, then, valuable to group similar task items under all circumstances, or none, or under some particular conditions? The object of the next chapter is to seek answers to this question.

Chapter 4

Effect of spatial structure on propensity reinforcement

4.1 Introduction

4.1.1 Aims of this chapter

In the previous chapter, it was found that the mechanism of self-reinforcing propensities for tasks can lead both to specialisation and to an ability to respond to changing conditions, albeit with a certain amount of trade-off between the stability of specialisation and the speed of response.

However, a worker using this mechanism could only specialise and maintain specialisation upon a task that constituted around half or more of all encounters. With this restriction, the mechanism is only likely to be effective (and therefore only likely to occur) when two tasks are present, or at least when one task of two or three is significantly more abundant. (It should also be recalled that the mechanism can only serve any purpose if specialisation is actually beneficial.)

The results in the last chapter were obtained using the assumption of random encounters between workers and tasks. As discussed there, in various cases it is reasonable to assume random encounters, but more frequently encounters deviate materially

from randomness. Within the nest, especially, there is often a high degree of ordering (e.g. Winston, 1987, Seeley, 1995 for honey bees; Franks & Sendova-Franks, 1992, Sendova-Franks & Franks, 1993, Sendova-Franks & Franks, 1995, Tschinkel, 1999 for ants) related to the proper care of the brood and the storage of food. Consequently task stimuli may exhibit spatial structure in the form of clustering: an item of a given task is more likely to be found near items of the same type than items of other types.

If task items appeared in clusters, then a worker might be able to specialise on one type of item, even if it formed a low proportion of the overall task mix, simply because it could be locally common. The aim of this chapter is therefore to explore the effect of spatial clustering, or clumping, on the propensity reinforcement mechanism introduced in the previous chapter.

4.1.2 Existing models of clumping

Over the last two decades, the importance of spatial structure in fields such as ecology and epidemiology has been increasingly appreciated. Specifically with regard to clumping, various models have been proposed; see Levin *et al.* (1992) and Pielou (1977) for a number of examples. The work has generally had one of two motivations:

1. Given a population, how can we determine how clumped it is?
2. What distributory processes cause natural populations to be clumped?

It turns out that answering the first question is not at all straightforward. Unlike some terms, such as 'density', 'size' or 'variance', which denote a specific statistical quantity, there is no single way to measure clumping, and the degree of clumpedness of a population depends on what measure is used (Pielou, 1977). To put that another way, clumping can be defined in different and mutually incompatible ways.

Asking, "What can we use as a statistical measure of clumpedness?" and, "How can we model the clumping processes of populations?" are virtually the same question in different guises, since a statistical measure of clumpedness requires a statistical model of clumps, and conversely to model clump formation requires that the degree of clumpedness produced be in some way measurable.

4.1.3 A general approximation of clumpedness

Neither of these types of work altogether matches the problem we wish to answer here, which is, for a given spatial structure to a population, what is the effect on encounter probabilities? So, rather than choosing one from among the many available models of clumped distributions, a simple assumption is made to simulate the general effects of clumping, and its effects are explored.

A simple approach to modelling encounters with clumped populations that can be used without explicitly modelling space is to assume that, having just encountered an item of one type, a worker's probability of encountering the same type again is elevated and the probability of other types reduced, in comparison to what those probabilities would be if they were proportionate to task abundance.

4.2 Methods

Responses to items encountered are modelled in exactly the same way in this chapter as in the previous. The only change is in calculating the probabilities of encounters to simulate the effects of spatial structure.

Imagine that a worker has most recently encountered an item of task i, and let its probability of encountering task i when task items are randomly distributed be denoted by x_i. Then, let the probability P_j of encountering next an item of type j, $j \neq i$, be given by

$$P_j = x_j c \,, \tag{4.1}$$

$0 < c \leq 1$, where c can be thought of as the clumping parameter; $c = 1$ is equivalent to random distribution of task items, and lower values of c correspond to increasingly clumped distributions. It follows that the probability P_i of re-encountering the same task type is

$$P_i = 1 - (1 - x_i)c \,. \tag{4.2}$$

This satisfies the condition that $\sum_{i=1}^{N} P_i = 1$ if $\sum_{i=1}^{N} x_i = 1$. (N is the number of task types.)

As with the previous chapter, analysis is made easier and computation time reduced by looking at the behaviour of a single worker. If a single worker is examined, and is considered, when clumping effects are neglected, to have equal probability of encountering all task types, then

$$x_i = 1/N \,.$$

The task type encountered on the first timestep is selected at random. For examining behaviour of groups, x_i will be taken from the encounter probability model used in the

previous chapter, so that

$$x_i = \frac{T_i}{T_{\text{total}} + \alpha N}$$

where T_i is the total number of items of task i, T_{total} the total number of items of all tasks, and α a parameter determining the area within which the items are present. (See previous chapter, p. 66.) In this model, encountering nothing is treated in the same way as encountering a task: the probability of encountering nothing at the next timestep is elevated and the probability of encountering each task is reduced. From the point of view of encounters, 'nothing' is simply another task type.

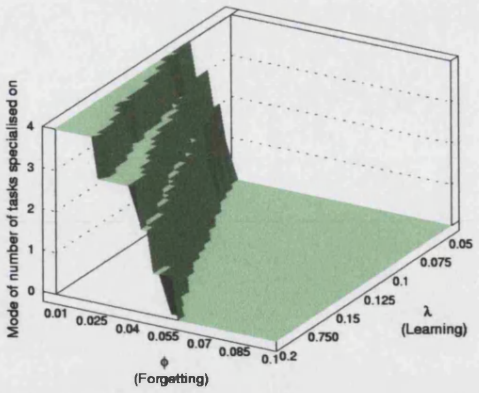
4.3 Results

The question this chapter is intended to answer is whether spatial structure can permit specialisation on a task that represents less than half of all task items, as this did not happen when tasks were randomly distributed. The method used to examine specialisation in the previous chapter was to measure the difference between a worker's propensity for one task and its propensity for the other. When there are more than two tasks, a different measure is needed. Here, the mode of the number of tasks for which the worker had a propensity greater than 0.5 was used: this gives an approximate indication of how many of the available tasks the worker is performing. Figure 4.1 shows the results of this for four tasks. Clearly the effect of clumping is to permit, for part of the parameter space, a single task to be specialised on even though that task only represents a quarter of all encounters. Note that, when $c = 1.0$ (no clumping effect), there is virtually no combination of λ and ϕ for which the most common number of tasks specialised on is 1.

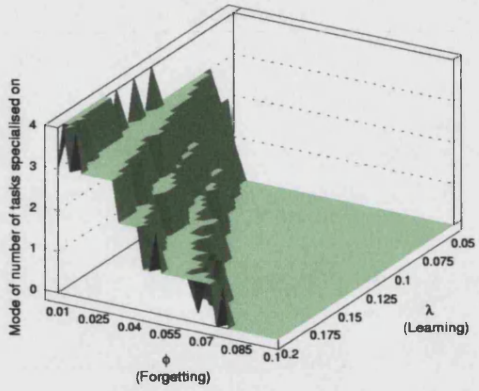
In the previous chapter, it was found that propensities tended to be either quite high and close to 1, or quite low and close either to zero or to R. Should this remain the case, then testing whether propensities are greater or less than 0.5 is a reasonable way to measure specialisation. The assumption therefore needs to be verified by looking at some traces of individual propensities, for the part of parameter space that is of interest because specialisation on a single task seems to be occurring.

Figure 4.2 shows an example of the dynamics of individual propensities, and it can be seen indeed that specialisation is genuinely on a single task at most times. However, it is also notable that the stability of this specialisation seems reduced in comparison with what was observed for similar λ and ϕ values in the previous chapter. Comparing the stability of specialisation for the same values of λ and ϕ when $c = 0.2$ with that when $c = 1.0$, with two tasks, the difference is clear (Figure 4.3). (The comparison effectively cannot be made with four tasks, since specialisation does not occur with four tasks when $c = 1.0$.)

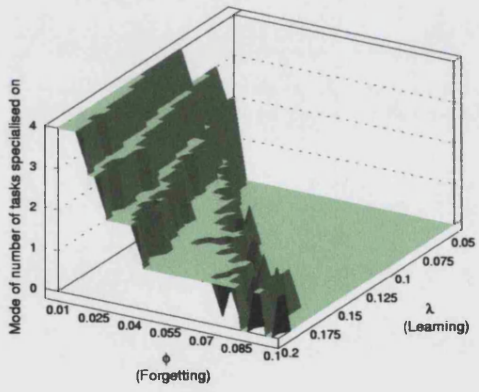
Finally, what effect does clumping have on responsiveness? We saw in the previous chapter that the mechanism's responsiveness to changing task demand must be explored by modelling a group rather than a single individual, in order to be understood correctly. Therefore, a group is modelled again here. The method used to measure



(a)



(b)



(c)

Figure 4.1: The number of tasks 'specialised' on across λ and ϕ parameter space at different degrees of clumping. A worker was supplied with task items as described in the text for 8000 timesteps, at the end of which the number of tasks for which it had a propensity greater than 0.5 was recorded. This was repeated across 20 replicates and the mode taken for each point on the graph. $R = 0.2$, starting propensity for each task 0.2, $N = 4$.

(a) $c = 1.0$, i.e. no clumping (the model is identical to the previous chapter).

(b) $c = 0.2$.

(c) $c = 0.1$.

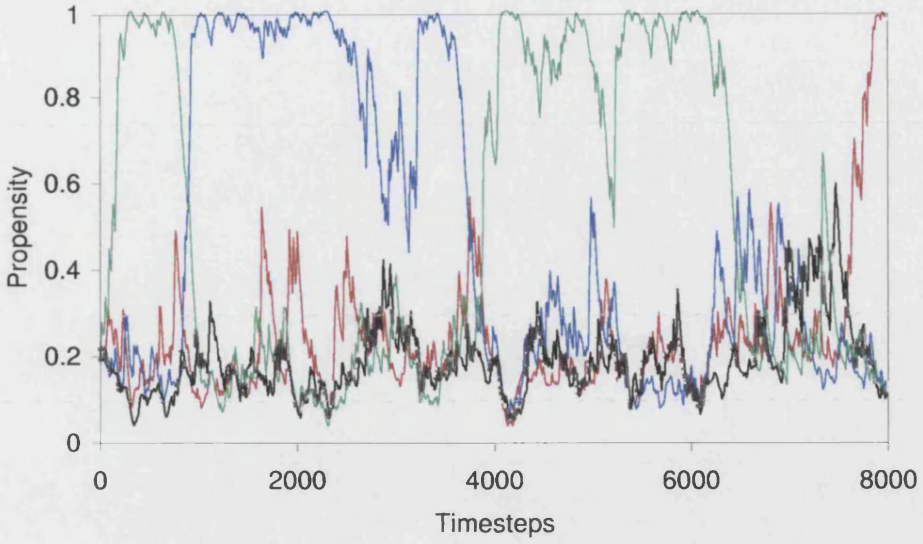


Figure 4.2: Evolution of individual propensities when there is clumping, with four tasks. $\lambda = 0.1$, $\phi = 0.0225$, $R = 0.2$, $c = 0.2$, starting propensity for each task 0.2.

responsiveness is the same as that used in the previous chapter, except that instead of supplying one task and adding a second, three tasks are supplied before adding a fourth. Figure 4.4 shows the results. In the zone corresponding to specialisation on one task, response times are around one to two thousand time steps, which compares unfavourably by a factor of five to ten with the response times found in the previous chapter, when adding a second task with no clumping effect.

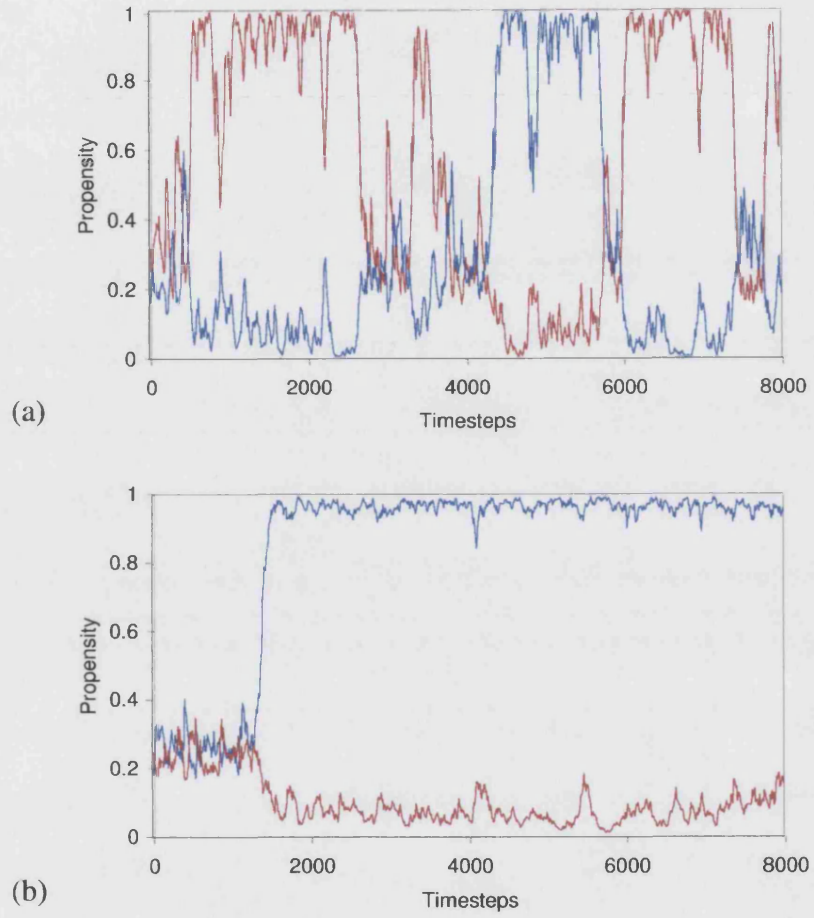


Figure 4.3: Evolution of individual propensities with two tasks, with and without clumping. $\lambda = 0.1$, $\phi = 0.05$, $R = 0.2$, starting propensity for each task 0.2.

(a) $c = 0.2$ (with clumping).

(b) $c = 1.0$ (no clumping).

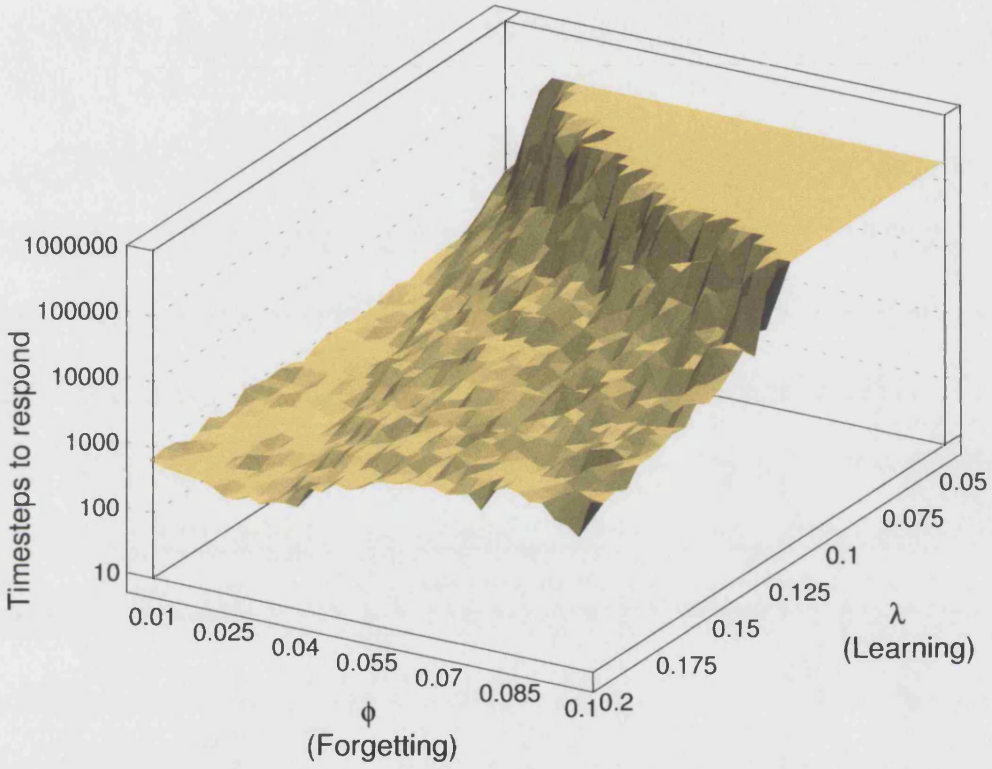


Figure 4.4: Time taken for a group of workers to respond to the introduction of a fourth task. The simulation was run with 3 tasks for 4000 timesteps before introducing the fourth, and the number of timesteps before the mean propensity for the new task reached 0.25 was counted. When the mean propensity for the new task reaches $1/(\text{no. of tasks})$ (here 0.25), it has reached parity with the others, hence a response can be considered to have occurred. $R = 0.2$, $c = 0.2$, $\alpha = 200$, $N = 20$, $w_i = 5$ except that $w_4 = 0$ up till $t = 4000$.

4.4 Discussion

The results above show that it is indeed possible to have specialisation on tasks which form much less than half of total task demand, when tasks are structured into clumps.

From where does the increased specialisation come? Why does the clumping effect allow workers to specialise on tasks that form only a quarter of the total available? Clumping causes specialisation to occur on a task whose levels would otherwise be too low to induce specialisation, yet it does not increase the proportion of encounters with that task. It is true that, in the short term, because the worker is likely to encounter the same type repeatedly, it may encounter a given type disproportionately often. Over longer timescales, however, the tasks are equal: although the worker can encounter the same task several times in succession, and become specialised on it, once it does encounter a different task, it is likely then to encounter that different task several times in succession. There is no bias towards the task on which the worker has specialised, in other words no feedback between the worker's propensity for its task and its probability of encountering it.

The increased specialisation happens simply because clumping increases the probability of uninterrupted sequences of a single task type, which are necessary to set up specialisation. For precisely the same reason, specialisation is less stable under clumping, since uninterrupted sequences of the 'wrong' task type are also more likely (although a specialisation, once established, can survive several successive encounters with tasks that are not specialised on).

As well as decreased stability of specialisation, a second cost of clumping (for this mechanism) is increased response times. These can be thought of as a consequence of reduced sampling quality. In effect, the propensity reinforcement mechanism uses task encounters to assess task abundance and thereby respond to inequalities in the abundance of different tasks. It has two goals which are fundamentally incompatible and cannot be reconciled without compromise: firstly, to specialise stably on one task, and secondly to be able to change tasks when another task becomes more urgent. Task item encounters reflect task abundance, but also contain randomness. Therefore, stability requires ignoring a certain amount of fluctuation. Since it is impossible to separate meaningless (i.e. random) fluctuation from meaningful fluctuation (i.e. due to actual changes in task abundance), increased stability means decreased responsiveness. Al-

though a feature of the present model, this trade-off is probably universal as it is a consequence of using encounter rates to determine behaviour.[1]

Here, the reason that clumping degrades sampling quality is that encounter rates, besides reflecting task abundance and including randomness, also reflect what task was encountered previously. Thus the information content of the signal is reduced. In concrete terms, a worker can fail to experience increased encounters with a particular task because it is 'trapped' into repeated encounters with some other task within a clump. The reduction in responsiveness may be somewhat exaggerated by the function used to model clumping, which has the feature that when one task is much less abundant than the others, the probability of re-encountering it, though higher than the probability of encountering it in the first place, is still very small. This may represent an excessive penalty: in effect it assumes that clumps become smaller as the task becomes less abundant. (The task's abundance is low when it is first introduced.) If this were not the case, response times would probably be better though still reduced from those seen with the random distribution used in the previous chapter. One possibility for future work, therefore, would be to examine variations in the assumptions about the effects of clumping with different task abundances.

Just as the trade-off between stability and responsiveness is probably universal, so this effect of clumping is probably also not peculiar to the present model, but a general property of task allocation systems. It has been remarked (Franks & Sendova-Franks, 1992) that clumping has benefits in that it can reduce travel times between task items for specialists. Against this benefit should be set the cost of reduced quality of information for workers. Probably some degree of spatial structure becomes essential for any group above five or ten individuals, simply because there is otherwise more information than each can process. However, some compromise between maximising sampling of the environment and minimising variety of encounters for workers (which is essentially what spatial structure strives to achieve) will always have to be reached.

In summary, then, the results from this chapter show that spatial structure can be valuable in structuring the input that workers receive, but that the structure comes at a cost of reduced responsiveness to change. If a time step is taken as being something between around half of a minute to several minutes, then the response times in the

[1]There is a large literature on optimal foraging and predation strategies, begun by the seminal papers of McArthur & Pianka (1966) and Charnov (1976), which whilst not conceived as social insect-specific is nonetheless relevant. Begon *et al.* (1996, pp. 339–368) provide an excellent introductory review; see also Pyke (1984) and Krebs & Davies (1987).

specialisation zone are increased to something between one or two hours and a day, as against what would be a few minutes to one or two hours without clumping. A time scale of one or two hours is precisely that over which within-role task allocation should operate, since between-role switches operate more on a scale of days. If task demand is liable to change within such a time frame, the reduced responsiveness resulting from clumping of tasks would be quite significant. Certainly some tasks can change that quickly: flower resources for bee foragers, for instance. But we are interested here in tasks whose spatial arrangement social insects can order themselves; external resources, while often clumped, do not fall into that category. Within the nest, task demand may be more stable, making the cost of slower responsiveness less serious.

Real social insects indisputably do create a spatial structure for many tasks. If they are using a mechanism that resembles propensity reinforcement, they are doing so despite the costs. Some tests for propensity reinforcement-like task allocation mechanisms were suggested in the last chapter. The results here suggest that, whether or not propensity reinforcement turns out to be involved in any social insect task allocation, an integral part of understanding spatial structure in social insect colonies will be to understand its effect on the information available to workers.

Chapter 5

Case study of a task: Dynamics of fetching wall material

5.1 Introduction

5.1.1 Motivation for the work

The theoretical exploration of broad classes of task allocation mechanism can provide insights from one direction; complementary to it are empirical studies on specific cases of task allocation, which provide examples of how the problem has been solved under particular circumstances by biological evolution. Neither, of course, should be subservient to the other: whilst theoretical models are clearly meaningless unless they can be validated by reference to real systems, empirical studies of individual cases cannot lead to genuine understanding of the processes involved unless they are applied to a model of some kind, without which generalisation from the results cannot occur.

The aim of the work presented in this chapter and in Chapter 6 is, therefore, to take a specific task and to look at how individuals are allocated to it (or rather allocate themselves to it), and particularly to examine whether reinforcement is involved in the allocation mechanism.

Given that this thesis is principally concerned with short-term task allocation and with

situations where stochasticity has important effects, a suitable task would be one

- that involves a small number of workers,
- that (in nature) needs to be performed inconstantly and unpredictably, and
- from a practical viewpoint, that can easily be manipulated to bring about the circumstances under which it is required.

Such a task is the fetching of material for wall building in the ant *Leptothorax albipennis*.

5.1.2 Choice of case study

Study species

L. albipennis (Curtis) (=*L. tuberointerruptus* Bondroit; previously misidentified in Britain as *L. tuberum* Fabricius; Orledge 1998a) is a small ant, both in size of workers (3-5mm. long), and number of workers per colony (ranging from a few tens to, very occasionally, around 500). It is monogynous with most queens being singly mated (Partridge *et al.*, 1997; Pearson *et al.*, 1995), although it shows evidence of seasonal polydomy, with colonies occupying multiple nest sites during the summer (Partridge *et al.*, 1997). Workers are monomorphic, excepting some size variation (Blanchard *et al.*, 2000). In Britain, it nests chiefly in narrow crevices within friable rock (Orledge, 1998b), often constructing a perimeter wall of grit or sand to enclose the nest within the crevice (Franks *et al.*, 1992; Franks & Deneubourg, 1997; personal observation). These crevices are typically only 1-2mm thick.

Since they naturally use flat nesting sites, colonies can be kept in the lab in artificial nests made from two glass slides separated by a cardboard perimeter wall, allowing their behaviour to be observed at all times without creating a distortion from the natural nest geometry (Franks & Sendova-Franks, 1992; Franks & Deneubourg, 1997). This convenient nesting behaviour, their small size, and their relatively straightforward social structure make them an excellent study subject: they present a microcosm of sociality within the space of a few square centimetres. The ease with which they

can be cultured and studied means that there is already a substantial amount of information about their behaviour (e.g. Franks *et al.*, 1992; Blanchard, 1997; Franks & Deneubourg, 1997; Partridge *et al.*, 1997; Backen *et al.*, 2000; Blanchard *et al.*, 2000; Cox & Blanchard, 2000; Sendova-Franks *et al.*, in preparation). They also have a very appealing demeanour.

Study task

In part due to their apparent seasonal polydomy (Partridge *et al.*, 1997), and in part due to the inherent instability of their environment, colonies of *L. albipennis* probably have to emigrate into a new nesting site several times in the life of a colony. Construction of a perimeter wall for the new nest has important fitness benefits, as it protects the colony and particularly the brood from predation (in which larger social insect species probably figure largely—indeed a *Lasius niger* worker has been observed in the field attempting to dig through the wall of a *L. albipennis* nest; G. Orledge, personal communication).

Although building a wall is important, it is not the only task that occupies a colony at such a time: the process of brood sorting occurs concurrently (Sendova-Franks *et al.*, in preparation) and is thought to be important for well managed brood care (Franks & Sendova-Franks, 1992). It is therefore necessary for the colony to regulate the building effort so that a wall is constructed in a timely manner without drawing off too much effort from other activities. Where the fetching of material with which to build is concerned, there is a further disincentive to large numbers of workers being involved in that it requires spending time outside the nest and is therefore dangerous.

The task of fetching wall material is suitable for investigation here because it needs to be performed inconstantly, because the number of workers involved does in fact appear to be small (perhaps as low as one or two, at least at any one time; Croucher, 1993; Franks & Deneubourg, 1997, N. R. Franks, personal communication), and because it can easily be provoked in the laboratory by destroying a nest housing a colony and offering the colony a new nest that is not completely walled, along with a nearby supply of material for building. This provides a close mimic of a natural emigration where, as mentioned, the nest cavity is of similar form and where also, their immediate surroundings being rock, workers might often have to travel some centimetres to find a source of building material.

Why concentrate only on the fetching of the material used to build the wall, excluding the shaping of this material into a barrier? Previous studies (Franks & Deneubourg, 1997; Franks *et al.*, 1992) and personal observation suggested that nest wall building in *L. albipennis* shows signs of what Ratnieks & Anderson (1999a) describe as 'task partitioning.' Task partitioning essentially involves the division of a single task (usually foraging) into subtasks performed by different workers. A typical example of task partitioning is found in several species of leafcutter ant in the genus *Atta*, which divide the task of harvesting leaves into three stages: cutting and letting drop leaf fragments, gathering of fallen fragments into caches located on trunk trails, and retrieval from the caches to the nest.

In the building behaviour exhibited by *L. albipennis*, there appears to be a similar division: wall material is fetched from the source outside the nest and deposited within the nest, usually in an area between the brood cluster and the zone where the wall later appears.[1] Subsequently the material is moved outwards by workers within the nest to a position abutting such wall as yet exists. Franks & Deneubourg (1997) state that a worker bringing material into the nest 'drops it within a distance of one or two of its own body length from the cluster of its nestmates... The ants that retrieve building material from the outside world rarely if ever pick up a stone that they have dropped inside the nest. The ants that remain in the nest... are, however, frequently seen to pick up stones that are close to them and bulldoze them outwards again.' (Thus the zone where stones are dropped forms a cache, analogous to those used by leafcutter ants for their forage; Hart & Ratnieks, 2000.)

The fetching of material and its arrangement into a proper wall, then, constitute two separate processes, probably carried out by different sets of workers (though perhaps with some overlap between the two sets). They can therefore be treated as separate tasks. Although a useful way to look at the logistics of gathering material, the idea of task partitioning is based on a misconception that some sequence of activities can be *objectively* considered as a single task by any means other than observing whether the sequence is consistently performed in its entirety by single individuals; it is misleading to differentiate between a 'single task' where parts of the sequence are performed by different workers, and a group of two or more tasks that have some interdependence

[1]One might wonder how the ants could consistently manage to drop stones behind the wall, when that wall has not yet formed. Franks & Deneubourg (1997) and Franks *et al.* (1992) suggest that this results from ants using the brood cluster as a mechanical template and 'pacing out' the distance from it to the wall, but an alternative and intriguing possibility put forward by Cox & Blanchard (2000) is that CO_2 or some other volatile substance produced by the brood cluster acts as a gaseous template, giving the ants a form of positional information within the nest.

(see Chapter 2).

The fetching task, rather than the arrangement of fetched material into a wall, was chosen because it promised to be simpler to observe and quantify. Insofar as it involves fewer workers, it is also more interesting, as the problem of regulation becomes more acute. There is an *impasse*: if regulation is accomplished by having a very small group of workers that have an intrinsic predisposition to fetch material, this group would be subject to severe stochastic effects making its size difficult to manage. (It has been suggested, e.g. by Fuchs & Moritz, 1998, that multiple mating in honeybees occurs to ensure the presence in the hive of rare but important 'specialist' genotypes; this is unlikely to be occurring in *L. albipennis* with its low mating frequency.) On the other hand, if no particular workers have a predisposition to the task, what is to prevent all or none from performing it?

Sendova-Franks *et al.* (in preparation) introduce a model where the regulation of three tasks associated with emigration in *L. albipennis* is regulated by competition between them. The tasks concerned are transport of other workers and brood into the new nest, brood sorting and building (including fetching). The model's variables comprise amounts of each task left to complete and numbers of workers engaged in each (the former shrinking more rapidly as the latter is larger). When the rate at which workers pick up a task depends not only positively on the amount of that task available but negatively on the amounts of the other two, and the model is appropriately parameterised, the tasks are performed in order with mass transitions and little overlap, as is seen in *L. albipennis*. The model assumes that workers are in principle available to do any of the three tasks; it would be useful, though somewhat beyond the aspirations of the present study, to discover whether this is in fact the case. An important question for such a mechanism is how competition between tasks could operate. Sendova-Franks *et al.* (in preparation) suggest that builders could be inhibited by the physical disturbance of transporters entering the nest, but it is not clear how brood sorting might inhibit building.

5.1.3 Aim of the experiment

The experiment presented in this chapter aimed to uncover information about the allocation of workers to the task of fetching wall material by using individually marked workers and observing the identities of workers that performed the task during re-

peated episodes of forced emigration and consequent building. By discovering which individuals are engaged in the task on successive occasions, it should be possible to distinguish between two opposing hypotheses: that the workers involved come from a very small set of specialists, or that they are a random selection from the outside-nest workers (i.e. all those workers that venture occasionally outside the nest, some 30–50% of the total).

5.2 Methods

5.2.1 Colony collection and culture

Colonies of *L. albipennis* were collected on Portland Bill on 8th May 1998. They were housed in the lab in nests made from two 51mm × 76mm glass slides, with a piece of cardboard 0.7mm thick sandwiched between them and cut to form a nest wall, with inner nest dimensions of 38mm × 24mm × 0.7mm and a nest entrance 4mm wide. Each nest was placed in a 10cm × 10cm Petri dish, with 18mm high walls which were painted with Fluon® (PTFE suspension; Whitford Plastics Ltd, 10 Christleton Court, Manor Park, Runcorn, Cheshire WA7 1SU) to prevent ants from escaping. The colonies were fed *ad libitum* on water and 10% honey solution, provided in small tubes plugged with cotton wool and changed weekly, as well as with 3–4 larvae of *Drosophila subobscura* weekly.

All the workers in each colony were marked by applying three minute spots of coloured paint (Pactra R/C polycarbonate model paint, supplied by Fred Coulson Models, 515 Wells Road, Bristol), one to the dorsal surface of the thorax and one to each side of the first gastral tergite. The marking procedure used by Sendova-Franks & Franks (1993) was followed. The marking was done in such a way that, should any worker lose any one of its paint marks, it would still remain uniquely identifiable. With s paint spots of c colours, it is possible to mark $c^s - 1$ individuals within this constraint; here up to 11 colours were used, permitting up to 121 workers per colony to be thus marked.

The four colonies used here are referred to as Colonies 3, 5, 6 and 9, and had 80, 61, 105 and 110 workers respectively when marked.

5.2.2 Experimental procedure

Colonies were fed 24h (i.e. water and honey water tubes refreshed, and larvae supplied) before each experiment. The experimental arena was a Petri dish identical to those used to keep the colonies, except that it lacked a lid. Prior to each experiment, the arena was cleaned carefully with detergent and water, rinsed and dried thoroughly and repainted with Fluon. The experimental arena contained a nest made from two 51mm × 38mm

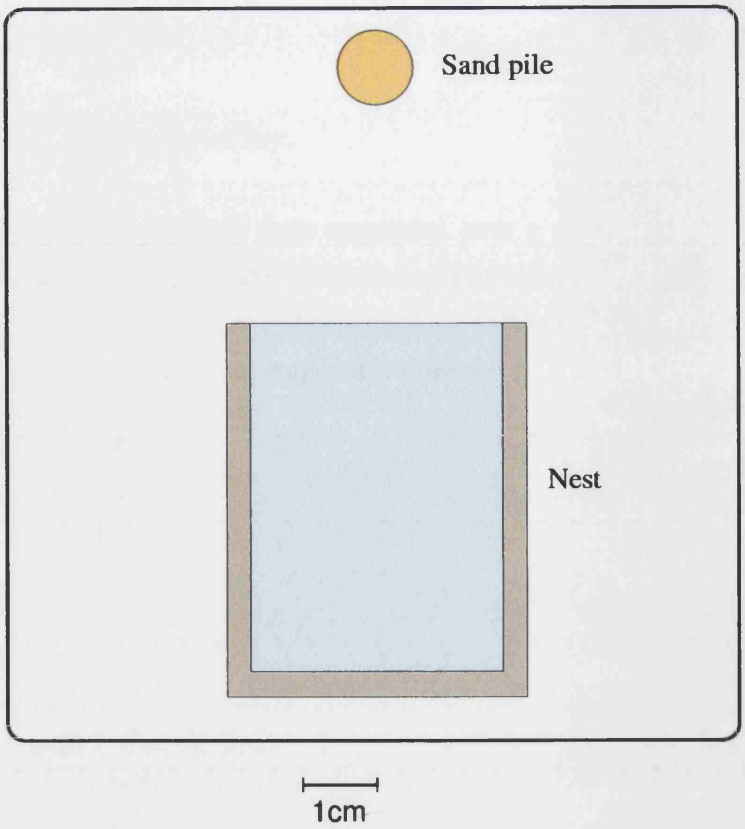


Figure 5.1: Layout of the experimental arena, shown to scale.

pieces of glass and a cardboard wall enclosing internal nest dimensions of 47.5mm × 32mm × 0.7mm, with one of the shorter sides left completely unwalled. On the opposite side of the arena, facing the open nest entrance, was placed a small pile of sand (grain size between 500μm and 800μm). Figure 5.1 illustrates the layout.

The nest containing the experimental colony was opened and all ants and brood were transferred into the experimental arena with the aid of a fine paintbrush. The experimental arena was then filmed (using a Panasonic SX30 Super-VHS video camera and a JVC HR-S9400 Super-VHS video recorder on BASF SE-180 tape) from 0–3 hours after introduction of the colony, again from 6–9 hours, and also from 24–27 hours and 48–51 hours if the nest wall remained sparse (approximately $<$ 200 sand grains) on the following days. While filming was taking place, at twenty minute intervals all ants visible outside the nest were identified with the aid of a hand-held binocular microscope; they were indicated on the video by pointing at them with a mounted needle whilst dictating their identities onto the video soundtrack. This was necessary because the S-VHS video system lacks the resolution to identify the paint marks on playback. Consequently identities have to be encoded in some way upon the video tape itself;

they cannot be established *post hoc*.

Each colony was emigrated on three occasions over a six-week period. After each emigration, water and honey-water tubes were reintroduced, and the colony was left in the experimental arena (with lid) and nest until the following experiment. Experiments were carried out during July and August for colonies 3, 5 and 6 and in September and October for colony 9.

5.3 Results

The results obtained comprise the times of all fetching behaviours that occurred during the filming sessions, and the identity of the ant concerned where available. Thus there are two dimensions to the data: the ID of each fetcher, and the temporal distribution of fetching. I shall present these largely separately, since it is difficult to represent both on a single table or graph.

The following table gives full details of the number of fetchers and the workers responsible.

Colony	Emigration	Session	Total fetches	Individuals	
				ID	Fetches
3	1	1	5		
				A	2
				x	2
				B	1
		2	0		
		3	2		
				C	2
	2	1	9		
				D	6
				E	2
				A	1
		2	2		
				F	2
		3	0		
		4	0		
	3	1	57		
				A	39
				G	13
				H	2
				I	1
		2	57		
				A	46
				C	7
				J	2
				K	1
				L	1

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Table 5.1: (see caption on p. 103).

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Colony	Emigration	Session	Total fetches	Individuals ID	Fetches
5	1	1	1	x	1
		2	53	x	26
				x	9
				A	3
				x	3
				x	3
				x	3
				x	2
				B	1
				C	1
				x	1
				x	1
		3	1	x	1
	2	1	15	D	11
				E	4
		2	61	F	28
				G	15
				H	5
				x	3
				I	2
				x	2
				J	1
				K	1
				L	1
				M	1
				x	1
	3	1	2	x	1
				x	1
		2	0		
		3	0		
		4	32	N	22
				x	8
				O	1
				x	1

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Table 5.1: (see caption on p. 103).

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Colony	Emigration	Session	Total fetches	Individuals ID	Fetches
6	1	1	17		
				A	13
				x	2
				B	1
				x	1
		2	14		
				x	4
				C	3
				A	2
				D	1
				E	1
				x	1
				x	1
				x	1
		3	0		
		4	22		
				x	13
				F	4
				G	1
				H	1
				x	1
				x	1
				x	1
	2	1	23		
				A	9
				x	4
				x	3
				x	2
				x	1
				x	1
				x	1
				x	1
				x	1

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Table 5.1: (see caption on p. 103).

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Colony	Emigration	Session	Total fetches	Individuals ID	Fetches
(6)	(2)	2	82		
				I	23
				x	19
				J	14
				G	12
				K	6
				x	4
				x	2
				x	1
				x	1
		3	11		
				L	5
				M	1
				N	1
				G	1
				x	1
				x	1
				x	1
	3	1	4		
				O	1
				x	1
				x	1
				x	1
		2	2		
				x	2
				x	1
		3	18		
				A	8
				E	1
				I	1
				x	1
				x	1
				x	1
				x	1
				x	1
				x	1
				x	1
				x	1

../..

Table 5.1: (see caption on p. 103).

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Colony	Emigration	Session	Total fetches	Individuals ID	Fetches
9	1	1	14		
				A	10
				x	2
				B	1
				x	1
		2	2		
				x	1
				x	1
		3	7		
				C	4
				D	2
				E	1
	2	1	8		
				A	2
				x	2
				B	1
				x	1
				x	1
				x	1
		2	7		
				x	1
				F	1
				G	1
				x	1
				x	1
				x	1
	3	1	14		
				x	4
				x	3
				x	2
				H	1
				x	1
				x	1
				x	1
				x	1
		2	7		
				I	2
				J	2
				K	1
				x	1
				x	1

Table 5.1: Fetches and fetcher identity in each filming session. A, B, etc. are identified individuals; x denotes an unidentified individual.

In principle, it is not possible to know whether two unidentified individuals are in truth the same worker or not. However, when both are observed at the same time they must be different individuals. By looking at which unidentified workers were tracked during overlapping periods within a filming session, it is possible to calculate both the smallest and the largest number of different fetchers that could have produced the observed tracks. In addition, it was occasionally possible on the video playback to discern some distinguishing feature of an unidentified worker which could be used to rule out the possibility of two workers being the same.[2]

Table 5.2 therefore summarises the information in Table 5.1, adding this extra information on the numbers that could actually have been present.

Of central interest is the number of fetchers that fetched in successive emigrations. It is only possible to answer this question for the workers that were identified. These data are summarised in Figure 5.2.

So far, the data presented have neglected the temporal information that was gathered in the course of analysing the video tapes. The primary aim of the experiments was to establish the identity of workers that fetched material, but in order to do so, the time of every fetching event had to be recorded prior to following the workers concerned till they were identified.

The results from these times of fetching events turn out to be the more interesting aspect of the data. It was noticeable whilst gathering the data that fetching trips tended to occur close together, with occasional longer intervals. This suggests that the behaviour is occurring in bouts. The traditional way to visualise bouts is by looking at a log-survivorship plot of interval length (Slater & Lester, 1982), although Sibly *et al.* (1990) argue that log-frequency plots are preferable because the points are independent. In either case, if events are governed by a Poisson process, that is they are occurring with constant probability per unit of time, the proportion of intervals of length between t and $t+1$ is $\lambda e^{-\lambda t}$, which gives a monotonically decreasing relationship on a log-survivorship or log-frequency plot. If there are two such processes co-occurring, one 'fast' process (λ large) and one 'slow' (λ small), the plot will instead be concave,

[2]One of the pecularities of VHS encoding is that the colour resolution is much lower than the fundamental resolution (of light and dark areas). Consequently, although most paint marks were invisible, it was possible to pick out unusually large or small, and unusually dark or pale workers. Light coloured paint marks (yellow or white or possibly light blue), if they were big enough, were also visible, but the exact colour of the mark was not.

Colony	Emigration	Session	Separate individuals Max / Min	Identified individuals ID'd / Shared
3	1	1	3 / 2	2 / 1
		2	0 / 0	0 / 0
		3	1 / 1	1 / 0
	2	1	3 / 3	3 / 1
		2	1 / 1	1 / 0
		3	0 / 0	0 / 0
		4	0 / 0	0 / 0
	3	1	6 / 5	4 / 1
		2	5 / 5	5 / 2
5	1	1	1 / 1	0 / 0
		2	11 / 5	3 / 0
		3	1 / 1	0 / 0
	2	1	2 / 2	2 / 0
		2	12 / 9	8 / 0
	3	1	2 / 2	0 / 0
		2	0 / 0	0 / 0
		3	0 / 0	0 / 0
		4	4 / 4	2 / 0
6	1	1	4 / 3	2 / 1
		2	8 / 5	4 / 1
		3	0 / 0	0 / 0
		4	7 / 6	3 / 0
	2	1	6 / 2	1 / 1
		2	9 / 5	4 / 0
		3	7 / 5	4 / 1
	3	1	4 / 2	1 / 0
		2	2 / 1	0 / 0
		3	11 / 7	3 / 2
9	1	1	4 / 3	2 / 2
		2	2 / 2	0 / 0
		3	3 / 3	3 / 0
	2	1	6 / 3	2 / 2
		2	6 / 5	2 / 0
	3	1	8 / 4	1 / 0
		2	5 / 3	3 / 0

Table 5.2: Numbers of individuals fetching and numbers identified. The columns 'Max' and 'Min' give the numbers of separate individuals that could have fetched, given the constraint that two individuals that were tracked separately at overlapping times could not be the same. The column 'ID'd' gives the number that were positively identified, and 'Shared' indicates how many of those were also identified in different sessions.

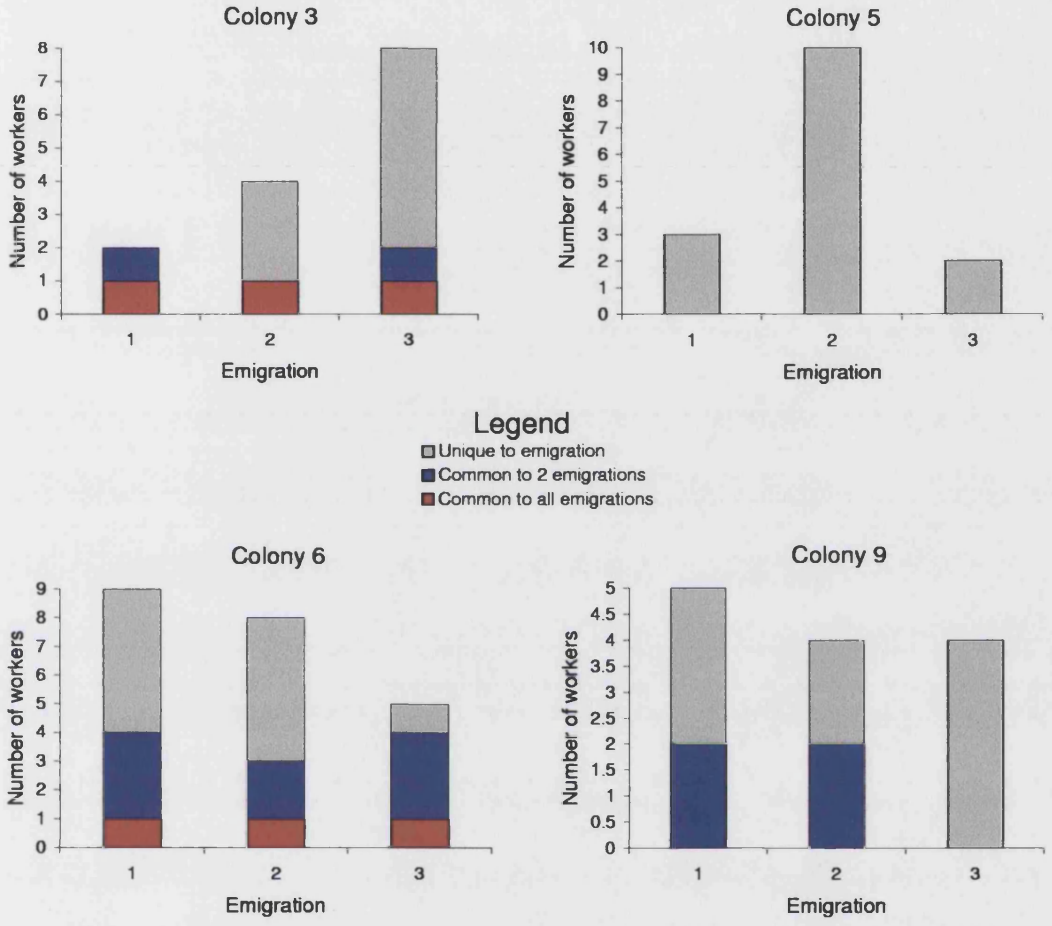


Figure 5.2: Number of fetchers unique to each emigration and common to two or three emigrations, for each colony.

comprising an initial rapidly-descending straight line due to the 'fast' process and a gently-descending straight line due to the 'slow' process, the two joined by an angle.

It is easier to illustrate the phenomenon graphically than verbally, which can be done easily since the inter-fetch interval data obtained here appear to fit the two-process bout model rather well. Figures 5.3 and 5.4 give log-frequency plots of inter-fetch intervals for pooled colony data and for selected individuals, respectively.

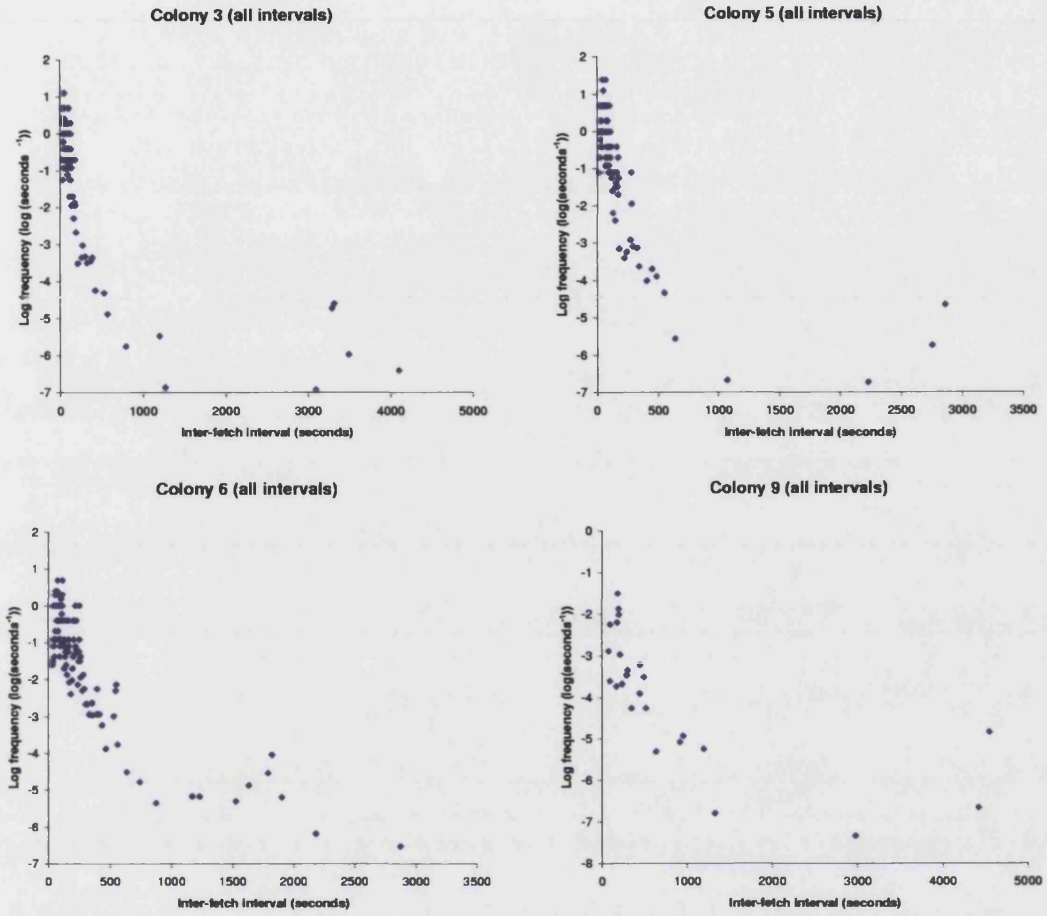


Figure 5.3: Distribution of inter-fetch interval lengths. Each graph gives, against the length of the interval between two successive fetches by the same worker, a plot of the frequency of intervals of that length. The frequency of an interval is calculated as the mean of the differences between its length and the length of the next longest and the next shortest intervals (or where an interval is the longest or shortest from that colony, then half the difference between it and its one neighbour).

These graphs show data for entire colonies, obtained by pooling the inter-fetch intervals of all workers in the colony. Figure 5.4 (following page) gives some plots for individual workers.

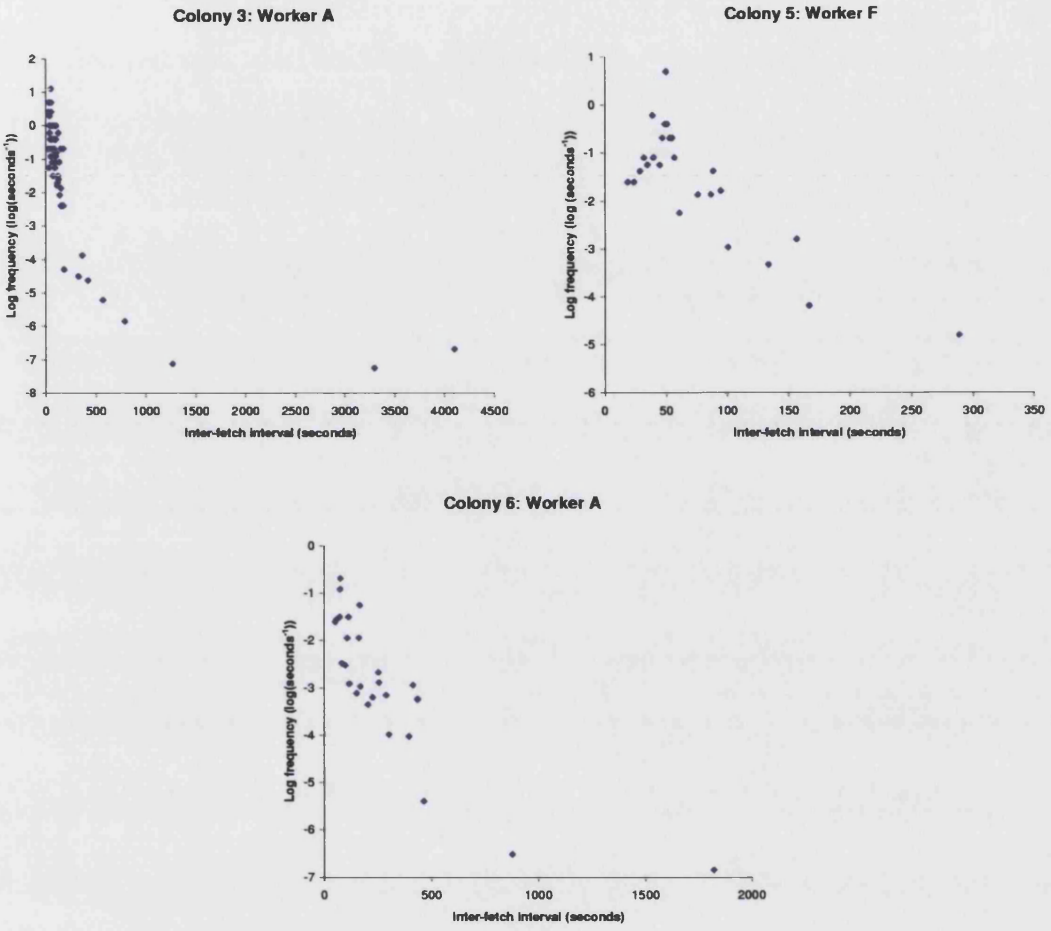


Figure 5.4: As Figure 5.3, but giving examples from individual workers. All workers that produced more than 25 inter-fetch intervals are shown.

5.4 Discussion

5.4.1 Identities

The results obtained in this experiment were a little disappointing with regard to the identification of workers. It had been hoped to obtain a near-complete tally of identities, thereby building a fuller picture of allocation to the task.

There is nevertheless enough data to suggest that the number of workers who may be available to do some fetching is fairly large in proportion to the colony size: probably at least 15–20, bearing in mind that the values in Figure 5.2 are based only on identified individuals. Whether all of these individuals are performing to a similar level is uncertain, but the data suggest not. Although there was relatively little overlap in the identities of individuals observed in different experiments, it was noticeable that those workers that were seen fetching in more than one experiment (Colony 5 excepted, since none were) tended to fetch more than those that were not (data in Table 5.1).

The results are therefore consistent with there being a small number of more dedicated fetchers who will fetch on all or most occasions that a wall needs building, accompanied by a larger group of more dilatory fetchers, any one of whom will only occasionally lend a hand (or rather a mandible). However, they are not substantial enough to be conclusive on this point. Further studies are really needed to pin down the problem.

The reason for the proportion of identifications being lower than anticipated was that it took some time to identify each worker, even with the aid of the binocular magnifying lenses; usually all paint marks were not simultaneously visible, or were in shadow, making it necessary to watch the worker for many seconds in order to get a definite identification. The rate of identification was of the order of two to three workers per minute. Moreover, at such a rate, the other workers changed positions between identifications, making it difficult to keep track of which remained unidentified. It was also not often possible to identify individuals forming the brood cluster within the nest, as they were too tightly grouped for their paint marks to be visible. Consequently, on the assumption that fetchers would, through the nature of their work, be spending a significant portion of their time outside the nest, only outside-workers and those near the nest entrance were identified.

The ants were noticeably disturbed during identification sessions (this is especially apparent on playing back the video recording at double or triple speed), and consequently the length and frequency of these sessions was a compromise between avoiding disturbance and getting reliable information.

In practice it transpired that, although fetchers did spend long periods outside the nest, it was also common for one to exit the nest, fetch some sand and return directly to the nest, then remain inside it. Indeed, though fetchers had been expected to come from the group of workers that congregates near the nest entrance (Boi *et al.*, 1999), when a fetcher entered the nest with sand, unless it left immediately to fetch more, it would often go right to the very back of the nest. Quite possibly, fetchers are observed fetching because they are workers that have a propensity to patrol the nest boundaries and to fetch material when they discover a breach. Because the ants within the nest are very tightly clustered, if a fetcher that is being tracked on the video tape enters the nest, it frequently blends into the crowd (which, being of largely uniform shade, forms a homogeneous brown mass on video playback) and is lost. Knots of workers would also form occasionally outside the nest, in which fetchers were sometimes lost.

In short, the level of successful identification was a product of the proportion of ants that were identified in any one identification session, and the length of time ants could be followed on playback before being lost. Both of these factors were lower than was desirable, but both were intrinsically limited by the technology available.

It is frustrating to note that, had the experiments been planned at the time of writing (2000) rather than some thirty months earlier, these problems would not have come about. In the intervening period, digital video recording equipment has entered the mass domestic market and is therefore a feasible tool for studies such as this one. The digital video (DV) format has a greater fundamental resolution than Super-VHS, but most importantly its colour resolution is in keeping with the fundamental resolution and therefore enormously better than VHS and Super-VHS. One cannot distinguish as many different colours on playback of DV tape as with the naked eye, but it is possible to distinguish about eight or nine (S. Pratt and E. Mallon, personal communication) which would be enough to identify fetchers on playback. The use of DV equipment is therefore strongly recommended for any future studies resembling the present one.

One other factor reducing the quality of the data slightly was that building was a little slow. This may have been because the nest was quite thin, with an internal nest height

of 0.7mm. This is the same as the thickness used by Sendova-Franks & Franks (1993, 1994, 1995), where the nest was deliberately made as thin as possible so as to restrict workers to purely two-dimensional movement. It was necessary there by reason of the technique used of stills photography with marked individuals, and is also advantageous here from the point of view of tracking workers by eye on video playback. Such a thin nest may also, however, induce building less strongly, since it is already too small to permit potential attackers such as *Lasius niger* to enter. Langridge (unpublished data) performed 30 emigrations on *Leptothorax albipennis* colonies, providing building material each time, with an internal nest height of 1mm, and building occurred on all occasions within 24 hours. A nest height of 1mm was therefore used in the following chapter's experiments. These did indeed provoke more fetching, although since the fetched material was continually removed from the nest in those experiments, the comparison is not an exact one.

5.4.2 Bouts

The data concerning inter-fetch intervals are more complete. As is apparent from Figures 5.3 and 5.4, there are two distinct, approximately straight-line portions of each graph. The exception is one of the individual plots in Figure 5.4 where there are not enough between-bout intervals to distinguish the second portion (caused by the 'slow' process).

In Figure 5.3, where data were had by pooling all of the inter-fetch intervals for each colony, the division between the two straight-line portions is less clear, with a tendency towards a curved region between the two. This is not surprising, since the parameters λ_f and λ_s for the 'fast' and 'slow' processes respectively (generating within-bout and between-bout intervals) will vary slightly among workers. Thus the curve seen is a superimposition a number of slightly different log-frequency plots. Differences could arise through workers having different characteristic walking speeds, different degrees of competence at navigating to and from the sand pile, different propensities to respond to the sand pile, and so on; in short, anything that alters the mean time between events.

The simplest way to analyse these plots is to fit a 'broken-stick' model to the data by eye; where the break occurs is taken as the bout criterion interval (BCI) (Sibly *et al.*, 1990). The BCI is used to determine whether an interval of a given length is most likely to be a between-bout interval or a within-bout interval, inasmuch as it is longer or

shorter, respectively, than the BCI. One's aim in selecting the BCI is typically, though not necessarily, to minimise the number of intervals that are misclassified. (Misclassifying some is inevitable: Slater & Lester, 1982; Sibly *et al.*, 1990).

Here, fitting a broken-stick model to the eye suggests a BCI of around 300–500 seconds, or approximately 5–8 minutes. Both Sibly *et al.* (1990) and Langton *et al.* (1995) have proposed procedures to find the best possible estimate for the BCI. However, it is doubtful whether applying them here would give a reliable answer. The data on inter-fetch intervals are biased by the fact that longer inter-fetch intervals are increasingly less likely, not only because they are intrinsically rarer, but because there is a greater probability of the ant being 'lost' (that is, not successfully tracked) and the interval consequently not being recorded.

One other interesting feature of the plots is that, on close inspection, it can be seen that the 'fast' process is not strictly a Poisson process since the frequency of extremely short intervals falls off rather than increasing. There is a lower limit on inter-fetch intervals imposed by the time it takes to carry a sand grain into the nest and return to the sand pile. Perhaps the within-bout intervals could be seen as being composed of this invariant (but individual-specific) minimal time plus a Poisson-distributed additional time caused by obstacles, encounters with other workers, and navigational hiccups.

5.4.3 Summary

Although the results concerning which workers perform fetching have not been as informative as hoped, this chapter nonetheless provides the first indications of the size of the pool from which fetchers are drawn. The clear demonstration that fetching occurs in bouts leads to some further ideas about the task's detailed regulation, which are described and tested in the following chapter.

Chapter 6

Regulation of fetching behaviour

6.1 Introduction

Chapter 5 looked in broad terms at how the task of fetching wall material is regulated. Its aims were to learn about the subset of the colony that became involved in the task, rather than the specific stimuli that elicited instances of fetching behaviour. In this chapter, we set aside the question of what determines which workers perform the task, and instead ask: for those workers that do perform the task, how is their performance regulated?

Although the answers to this question might be tied to the specific details of the fetching task, its principal features are not unique. These are: (1) individuals work independently; (2) the task can reach completion, at least till the next disturbance or emigration; (3) the source and sink of task material are physically separate. Examples that share at least two of these features include:

- comb construction in bees
- cell construction in wasp nests
- termite nest building
- retrieval of cached leaf fragments in leafcutter ants
- foraging from exhaustible sources such as from flower patches by bees

- daytime transfer of the brood to upper galleries to benefit from sun warming by ant species in temperate climates.

The experiments in Chapter 5 demonstrated clearly that the fetching of wall material occurs in bouts. The existence of these bouts suggests some potential points at which fetching behaviour could be regulated, and the experiments described in this chapter are aimed at assessing the rôle that these potential regulation points actually play. By 'regulation' I mean that a worker's behaviour changes according to the presence or absence of nest wall; a 'point of regulation' is a point at which the state of the wall can affect a worker's behavour.

6.1.1 Potential points of regulation

A bout of fetching requires a worker outside the nest to encounter a source of building material, to respond to it by picking up some of the material and returning to the nest with it, and immediately having done so to repeat the behaviour. In this there are three possible points of regulation.

- Firstly, workers may sense the absence of a nest wall and hence be induced to leave the nest in search of building material. This would manifest itself in an increased number of workers outside the nest when the wall is incomplete, which would increase the probability of one of them encountering a source of building material.
- Secondly, having encountered a source of building material, a worker's probability of responding to it by picking up material and carrying it back to the nest may be conditioned by its previous experience of the nest wall's state. This would manifest itself as an increase in the number of bouts of fetching when the wall was incomplete, if encounters of workers with building material remained at a constant level.
- Thirdly, on returning to the nest with building material and depositing it, a worker's probability of repeating the behaviour might depend on the state of the wall as the worker found it at that moment. This would be manifested as an increase in the length of bouts when the wall was incomplete.

Dependent upon the regulation points actually used, several scenarios can be envisaged. The one which posits least computational ability on individual workers is that workers produce the behaviour randomly at a low level, and when the behaviour is found to be 'successful' (because a worker returns to the nest with building material and is able to place it in a gap in the wall) it is then repeated. This resembles Frank's (1996; 1997) idea of adaptive systems in that a problem is solved by generating random variation and reinforcing 'successful' variants: workers could produce acts randomly from a large behavioural repertoire and those that were by some measure successful would be reinforced (i.e. repeated).

A possibility where the workers take a more active part in generating the behavour is that workers sense the absence of a wall and that this stimulates them to leave the nest in an active search for building materials, which they will then respond to when found.

Another possibility, where the workers are less proactive in generating the behaviour, is that workers are not specifically stimulated by the absence of wall to leave the nest, but that when they do encounter building material outside the nest, in light of their knowledge of the wall's state they are more likely to respond to it. This has the interesting feature that workers would remember the state of the wall without yet having encountered the stimulus (wall material) that makes such information valuable, suggesting (if this were a general feature in task allocation) that workers might be moving around with many pieces of information each stored against the possibility that it might become useful. In this scenario, a worker having once responded to building material, the length of the succeeding bout might follow a fixed pattern or might itself be responsive to the collection of further information about the state of the nest wall.

6.1.2 Aim of the experiment

The experiment described here was designed to identify whether each of these potential regulation points plays a rôle in regulating the fetching of building material, by providing colonies with nests whose walls were complete in some cases and incomplete in others, giving them a supply of building material, and establishing the numbers and lengths of fetching bouts and the numbers of workers outside the nest. From a knowledge of the relative importance of the three regulation points set out above, it should be possible to draw an approximate picture of the overall behavioural rules for the task.

6.2 Methods

6.2.1 Colonies

Six queenright colonies were collected on Portland Bill on 6th June 1999. Collection and colony housing methods before and between experiments were as described in section 5.2. Colonies were also fed as described in that section, until the experiments started, and in the same way but every three days once experiments had begun. (This was simply to provide fresh food the day before each experiment, since each colony underwent an experiment every third day.) After collection, the number of workers in each colony was counted; details are given in Table 6.1, below.

Colony	No. of Workers
10	35
11	49
12	107
13	113
14	70–75
15	120

Table 6.1: Colony sizes

6.2.2 Arenas and nests

Between experiments, colonies were kept in 'storage' arenas identical (aside from the addition of a lid) to those used for the experiments in Chapter 5.

The experimental arenas were larger than the storage arenas; their dimensions and layout are shown in Figure 6.1. As before, their walls were painted with Fluon® (PTFE dispersion; Whitford Plastics Ltd, 10 Christleton Court, Manor Park, Runcorn, Cheshire WA7 1SU). Each experimental arena contained a nest, held in position with two pieces of Blu-Tac, and a small pile of iron filings. The iron filings came from the departmental workshop, and a particle size range from 500μm to 800μm was obtained by seiving. To remove oil traces they were washed thoroughly, and to ensure that any filings brought into the nest by workers could be extracted magnetically, a magnet was used to select only the ferrous particles.

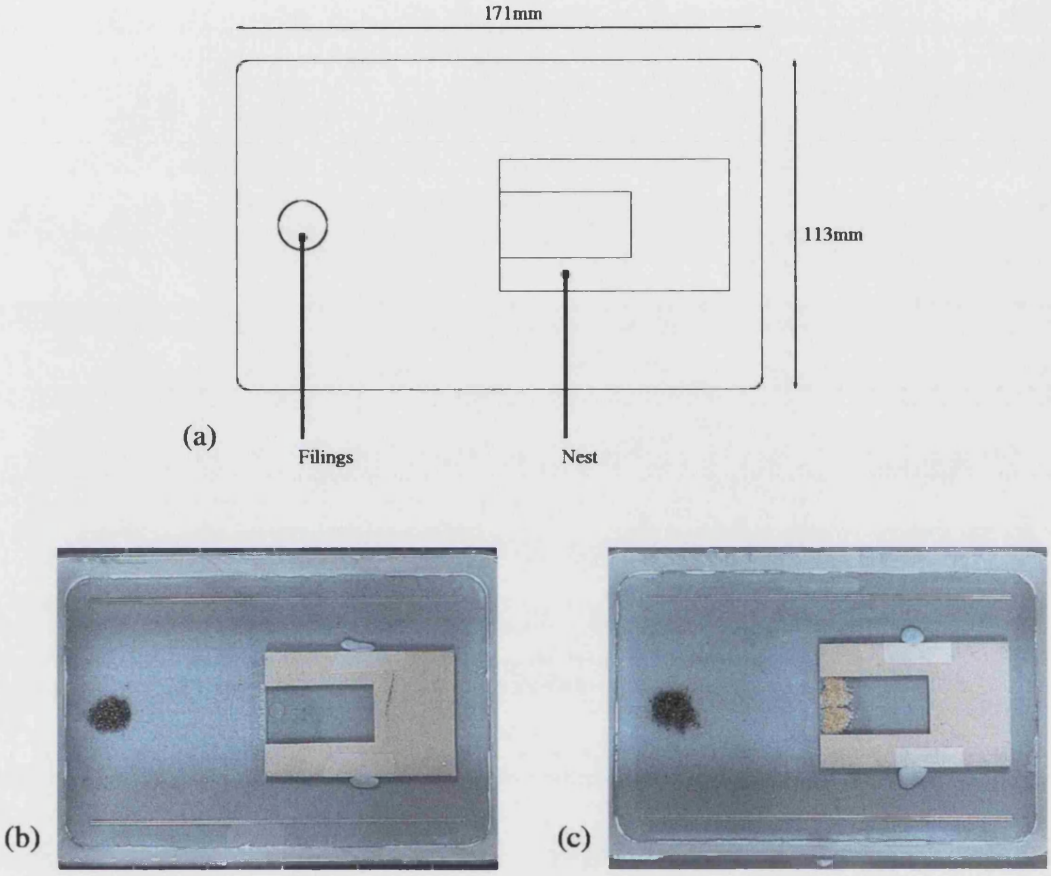


Figure 6.1: (a) Layout of experimental arena. (b, c) Video stills of test (b) and control (c) arenas, before introduction of colonies.

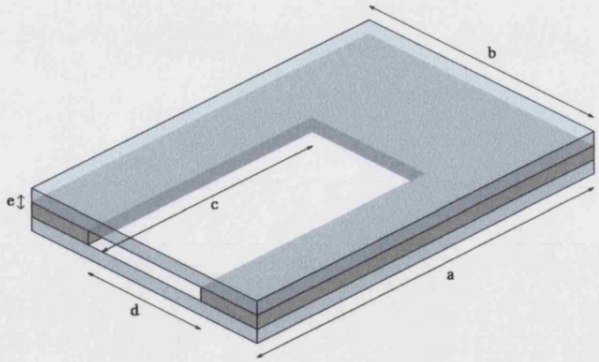


Figure 6.2: Nest dimensions: external a = 76mm, b = 51mm; internal c = 44mm, d = 24mm, e = 1mm.

Nest dimensions are given in Figure 6.2. As in the previous experiments, nests were made from a cardboard wall sandwiched between two glass slides held together with sticky tape. Note that the internal nest height is higher than it was in the experiments described in the previous chapter. It was thought that the relatively confined nest used there (0.7mm high) may have reduced the amount of building (see Discussion to that chapter).

Two types of nest were used. Nests for 'test' treatments were simply as indicated in Figure 6.2; nests for 'control' treatments had the added feature of a wall made of sand blocking the open end of the nest completely apart from a 1mm wide entrance passageway produced by inserting a mounted needle. (Figure 6.1 illustrates arenas set up with both test and control nests.)

6.2.3 Experimental treatments and filming

Two experimental treatments were used, referred to as 'test' and 'control' treatments. Aside from the differences in the nests used (see previous paragraph), both treatments were identical and consisted in the following.

Colonies were given fresh water, honey water and *Drosophila* larvæ 24 hours before each experiment. An experimental arena was prepared, containing a new nest and a small pile of iron filings. (Dimensions, construction and so on of these are detailed above in section 6.2.2.) A slip of paper was placed over the new nest, to reduce light levels inside and thereby encourage the ants to move into it.

The old nest, holding the majority of the colony, was removed from the storage arena in which the colony had been kept, and the tape holding it together was removed. It was placed directly on the new nest and in the same orientation, and the upper slide and cardboard wall were removed, leaving the colony exposed on the lower slide. Any ants remaining in the storage arena were then transferred into the experimental arena. The water and honey water tubes, however, were left in the storage arena; neither food nor water was provided in the experimental arena.

The colony was then left for 30 minutes, or until the last brood item was moved into the new nest, whichever was the longer. The remains of the old nest and the slip of paper covering the new nest were removed, and the colony was filmed for 6 hours.

Every 15 minutes during the filming period, any workers outside the nest were counted. Every 30 minutes, a magnet was passed over the nest entrance, whether or not any iron filings had been brought in. The filings brought out on the magnet, if any, were removed and counted. (It is almost impossible to remove the filings unless the magnet is first wrapped in some thin non-magnetic material which can be slipped off; a paper 'glove' was constructed for this purpose.)

The filming apparatus was set up in duplicate so that colonies could be experimented on two at a time. Images were recorded using two Panasonic NV-SX30B Super-VHS–C camcorders and recorded onto standard 180 minute Super-VHS tapes (BASF SE–180) using a JVC HR–S9400E Super-VHS videocassette recorder (in long play mode, giving 6 hours of recording on a 180 minute tape at normal frame rate) and a Panasonic AG-TL700 Super–VHS timelapse videocassette recorder (in "12H L" mode, actually giving 15 hours of recording on a 180 minute tape at 5 frames per second). Figure 6.3 shows the general filming setup. The view from each camera during the experiment is shown in Figure 6.4.

When filming finished, any filings and/or sand in the nest were removed (the sand was simply tipped out). The nest was returned to its storage arena, followed by any workers that were outside the nest, and food and water supplies were restituted.

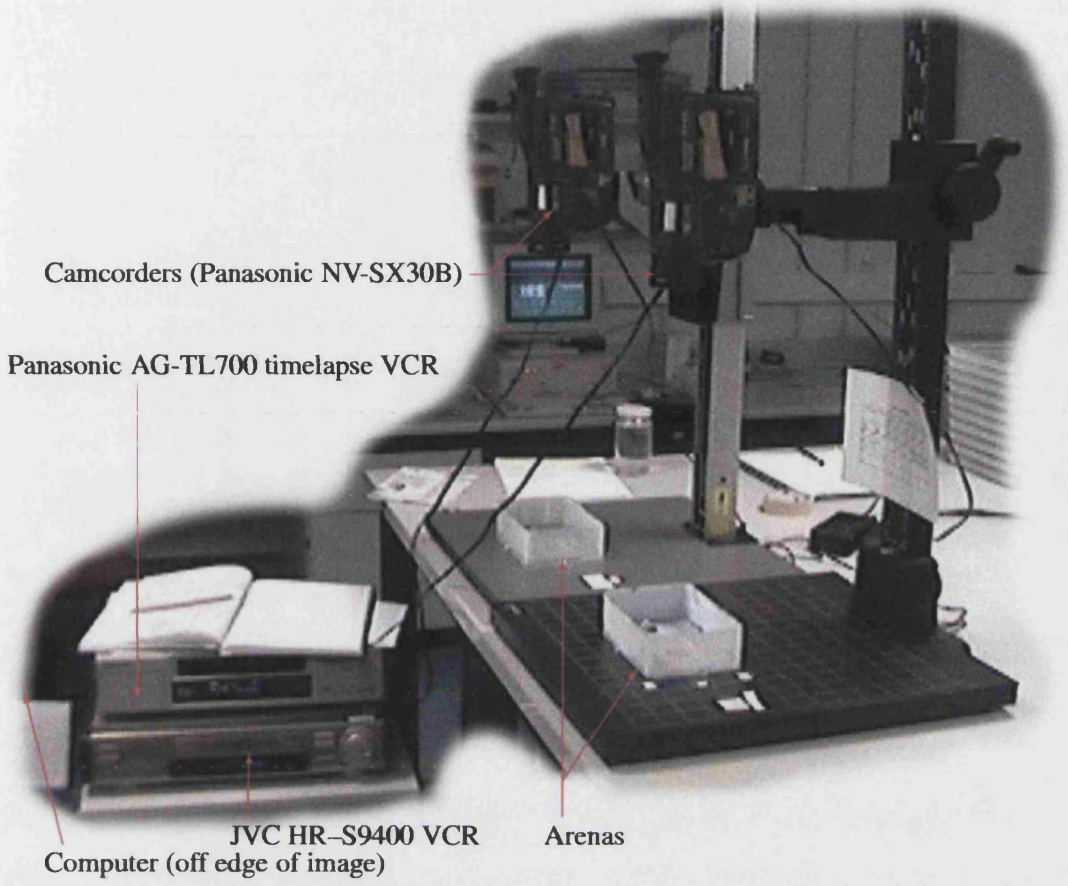
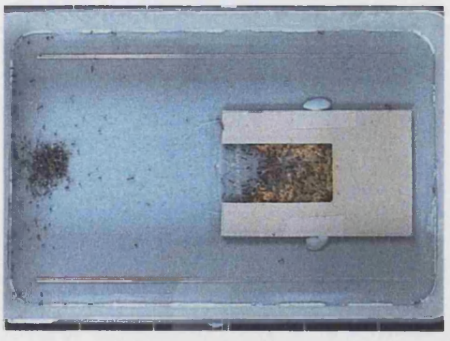


Figure 6.3: How the filming kit was set up.

(a)



(b)

Figure 6.4: Video stills from (a) a test and (b) a control experiment.

Mon	Tue	Wed	Thu	Fri	Sat	Sun
Jun 14	Jun 15	Jun 16 **13C** **15T**	Jun 17 **10T** **11C**	Jun 18 **12T** **14C**	Jun 19 **13C** **15T**	Jun 20 **10C** **11T**
Jun 21 **12C** **14T**	Jun 22 **13T** **15C**	Jun 23 **10T** **11C**	Jun 24 **12C** **14T**	Jun 25 **13T** **15C**	Jun 26 **10C** **11T**	Jun 27 **12T** **14C**
Jun 28 *13C* *15T*	Jun 29 *10T* *11C*	Jun 30	Jul 1 *13C* *15T*	Jul 2 *10C* *11T*	Jul 3	Jul 4 *13T* *15C*
Jul 5 *10T* *11C*	Jul 6 *12T* *14C*	Jul 7 *13T* *15C*	Jul 8 *10C* *11T*	Jul 9 *12C* *14T*	Jul 10	Jul 11
Jul 12 *12C* *14T*	Jul 13	Jul 14	Jul 15 *12T* *14C*	Jul 16	Jul 17	Jul 18

Table 6.2: Timetable of experimental treatments. Number denotes colony; T = test; C = control.

6.2.4 Sequence and timetable of treatments

Six colonies were used; each underwent two experiments under test conditions and two under control conditions. There are six possible orderings by which two treatments each of two types can be given, and one colony was assigned to each treatment sequence (Colony 10, TCTC; Colony 11, CTCT; Colony 12, TCCT; Colony 13, CCTT; Colony 14, CTTC; Colony 15, TTCC; T = test, C = control). Since the order in which the colonies were collected was arbitrary and can effectively be considered random, this constitutes a random assignment of colonies to treatment sequences.

The colonies underwent treatments at three day intervals. After the series of two test and two control treatments for each colony, a second identical series was carried out without a break (except for colonies 12 and 14, which had a break of one week). The same assignment of treatment sequences was used for this second series, and the protocol was identical, but only data on the numbers outside the nest were collected.

The complete timetable of colonies and treatments is given in Table 6.2.

6.2.5 Video analysis and classification of fetching behaviour into bouts

Videos were analysed in two stages. First, each video was watched from start to end (except for those half-hour sections where no material had been brought into the nest) and each time a worker brought an iron filing into the nest, the time the filing was picked up was recorded. In the second stage, each of these fetching events was revisited on the video; the ant involved was followed on the tape and if it performed further fetching trips without switching to another behaviour in the intervening time, these additional trips were held to form part of a single bout (and were removed from the pool of individual fetching occurrences that still required revisiting on the tape). "Another behaviour" is defined as any of the behaviours listed in Table 6.3.

The criteria for bout classification in Table 6.3 were arrived at as follows. Thirty-one inter-fetch intervals were selected from the previous year's set of experiments (Chapter 5), representing the full range of interval lengths from under one minute to over ten. The start of each interval was located on the videotape, and the tape was then played through; the ant concerned was followed, and its behaviours recorded. Since we know from the previous experiments that the bout criterion interval is in the region of five to eight minutes, those behaviours that consistently occurred in intervals longer than five minutes were included among the behavioural criteria listed in Table 6.3, while those that did not (which included brief interactions with nestmates, search behaviour outside the nest, and interactions with wall material other than fetching) were excluded. It is reassuring to note that the behaviours that appear not to mark the end of a bout are those which could most reasonably be expected to form part of the fetching behaviour 'program': search behaviour is occasionally necessary to relocate the nest entrance or the pile of filings; the fetching 'program' could well extend to making adjustments to existing wall material upon returning to the nest; and workers would be expected normally at least to check that other individuals encountered near the nest were indeed nestmates, without necessarily exiting from their current behavioural state.

Confidence in the criteria can be additionally reinforced by two observations. Firstly these criterion behaviours tended not to occur alone: either none occurred, in the shorter intervals, or more than one occurred, in the longer intervals. Second, these behaviours are not associated with longer intervals merely because of the time they take to perform. This might be the case, for instance, with the criterion of interactions

Behaviours considered to end a bout
Spends > 1 minute in brood group area
Interactions with workers/larvae in brood cluster
Immobile > 1 minute
Interaction > 1 minute long with worker in arena
Traversing pile of filings without picking up material
Attempting to climb wall of arena

Table 6.3: Criteria for bout analysis. Any of the behaviours listed was taken as evidence that the worker was no longer engaged in fetching behaviour.

lasting more than one minute. Clearly, on average, an inter-fetch interval that includes a minute long interaction with a nestmate will tend to be longer than one that does not. One might take an *a priori* view that interacting with nestmates is not part of the fetching task, and therefore must be classed as a separate activity. However, it is preferable, where possible, to ask the ant what she 'thinks' she is doing. Here, if the longer intervals associated with long interactions with nestmates are only longer than other intervals by the amount of time the interaction itself takes, this would suggest that the ant, despite being sidetracked by the interaction, is still in 'fetching mode' since she continues with it as soon as she is able. By contrast, if these intervals are disproportionately long, as indeed appeared to be the case, this suggests that the ants engaged in them are not continuing with the task they were doing prior to the interaction, and that therefore there has been a genuine change of behaviour.

Thus in the course of analysing each experiment, zero or more bouts were observed, each of these bouts consisting of one or more fetching trips (events).

The expression "bout length" will hereinafter refer to the number of events in a bout, rather than the time taken to complete a bout. This is because we are interested in the decision process of whether the fetching behaviour is repeated, rather than how long the trips take. Other factors (such as variable efficiency in navigating between the nest and the pile of filings) intervene in the length of trip but do not need to be considered here, as we are not immediately concerned whether they vary under the two treatments.

Treatment	Colony					
	10	11	12	13	14	15
Test 1	3.7083	11.7083	19.9167	32.75	17.0	24.25
Test 2	5.5	16.3333	31.4583	39.375	21.375	29.1667
Test 3	5.5	17.9583	29.875	46.6667	29.8333	29.125
Test 4	3.75	17.3333	24.4167	39.6667	26.3333	44.7083
Control 1	3.375	11.3333	20.9167	29.625	12.7917	23.0417
Control 2	4.2917	8.5833	29.8333	29.9583	20.4583	34.5833
Control 3	4.0	12.3333	24.9167	35.0	26.75	40.125
Control 4	2.125	15.9583	24.4167	43.6667	22.25	40.9583

Table 6.4: Mean numbers of workers outside the nest in each experiment.

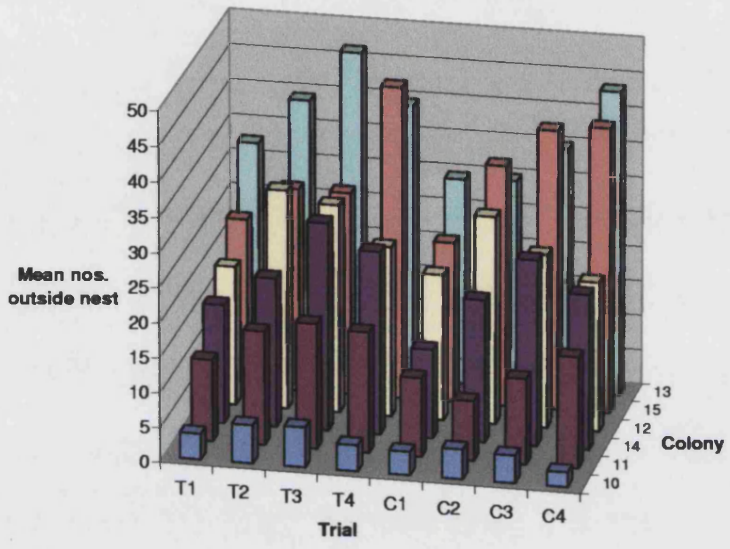


Figure 6.5: Mean number of workers outside the nest in each experiment.

6.3 Results

6.3.1 Numbers of workers outside the nest

The mean numbers of workers counted outside the nest during each experiment are shown in Table 6.4, and illustrated graphically in Figure 6.5. (Note that for this measurement, data are available from four trials per colony per treatment, whereas data for bout numbers and bout length are only available from two trials per colony per treatment.)

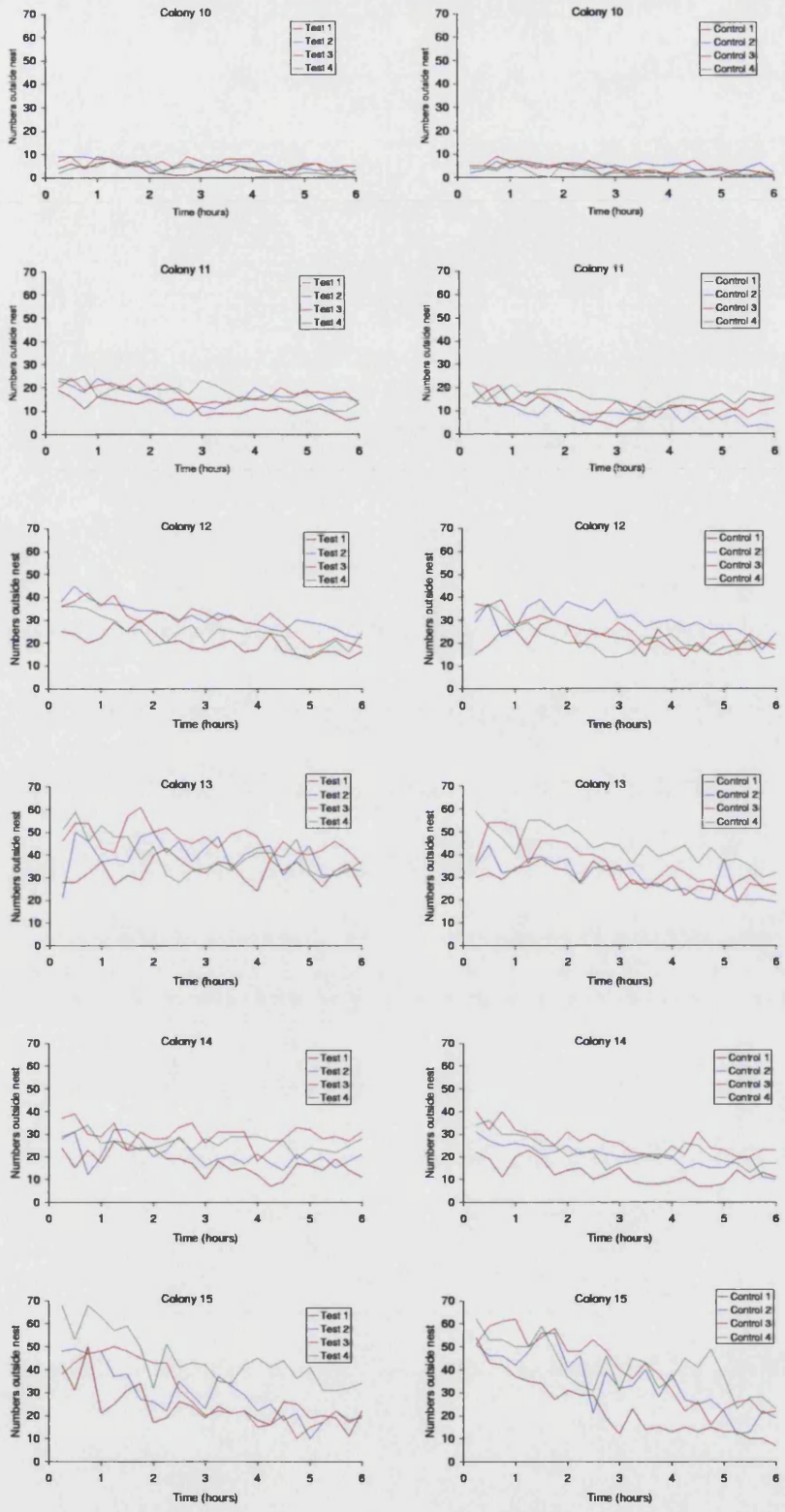


Figure 6.6: Timecourses of numbers outside the nest in each experiment. The left-hand column gives timecourses from experiments under test conditions, the right from controls.

Carrying out a two-way ANOVA on the mean number of individuals outside the nest during each experiment, treatment effect has a significance level of $P = 0.057$ ($F_{\text{treatment}} = 6.06$; two-way ANOVA on log-transformed data with treatment as a fixed effect and colony identity as a random effect). If the data are broken up by taking the means for each hour and comparing the mean numbers outside the nest during each experiment for a given hour, only during the last hour is there an apparently significant effect ($F_{\text{treatment}} = 6.11$; $P = 0.018$; two-way ANOVA as above). Furthermore, this significance level must be treated with caution, arising as it does from multiple unplanned comparisons. The problem is that, by using the mean numbers of workers outside the nest as a single observation per experiment, a lot of information is lost. A randomisation test using the procedure described below in Section 6.3.5 including all the observations taken at 15-minute intervals gives a surprisingly strong significance to the treatment effect of $P = 0.000001$. (Note that the *size* of the effect is nonetheless small: the average difference in number of workers outside the nest between test and control experiments is 1.9.)

This highly significant result cannot, however, be trusted. Admittedly, since the workers are quite able to move in and out of the nest over a shorter timescale than 15 minutes (and typically do so), it could be argued that data points taken at 15 minute intervals are independent. A simple thought experiment illustrates that such is not the case. Suppose that some colonies experienced more disturbance than others during emigration and consequently remained more agitated and had more individuals outside the nest for the duration of the experiment. A statistical test carried out on a per-experiment basis would correctly interpret the probability of this having happened at random. However, a test that took every 15-minute observation as a separate variable would consider it highly unlikely that all 24 observations in a single experiment had elevated values.

Consequently, confidence can only be placed in the tests carried out on per-experiment data. (A randomisation test carried out on the per-experiment data is actually weaker than the ANOVA, giving $P = 0.10$, but the result can be taken as broadly in line.)

6.3.2 Number of bouts

The number of bouts occurring in each experiment is given in Table 6.5 and illustrated in Figure 6.7.

	Treatment	
Colony	Test	Control
10	0 2	1 2
12	66 12	1 14
13	9 6	13 3
14	11 21	0 3
15	152 146	6 10

Table 6.5: Number of bouts observed in each experiment.

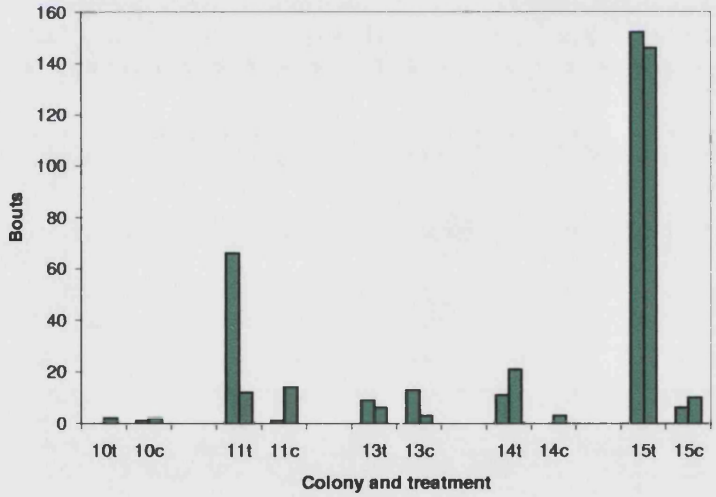


Figure 6.7: Number of bouts observed in each experiment (t = test, c = control).

The format of these data suggests a two-way mixed model ANOVA, as performed above on the mean numbers of workers outside the nest per experiment. However, the data actually obtained rule out an ANOVA because of the heterogeneity of variance within subgroups. This heterogeneity is not tractable to transformations such as log-transformation.

Neither are the non-parametric alternatives to two-way ANOVA appropriate: Friedman's rank sum test is designed for randomised-blocks designs which have one observation per cell (Sokal & Rohlf, 1995; here there are two) and the Scheirer-Ray-Hare extension to the Kruskal-Wallis test (Scheirer *et al.*, 1976) is only intended to stand in for Model I ANOVA (Sokal & Rohlf, 1995; here the model is mixed).

To overcome these difficulties, randomisation tests were used to test the conformity of the bout number data to the null hypotheses above. Test treatments in fact produced significantly more bouts than control treatments ($P = 0.008$, one-tailed randomisation test; see Section 6.3.5).

Since it has already been shown that there may be more workers outside the nest under test conditions, the question arises whether this effect would be sufficient to account for the increase in the number of bouts. If more workers are outside, there will be more encounters with the pile of building material, and therefore more bouts, even if each worker's probability of responding to the pile of building material on encountering it remains the same. The method of Manly (1991) (see Section 6.3.5) can be used to calculate 95% confidence limits for the size of the treatment effect on numbers outside the nest in those experiments for which bout data are available (that is, the first two test and the first two control experiments on colonies 10, 11, 13, 14 and 15). This method gives the 95% confidence limits as 1.01 and 2.95, the upper value representing a mean increase of 15% over the control conditions. However, since it is based on the randomisation test which it has been explained is flawed, these values are not reliable. Nonetheless, when numbers of bouts under test conditions were reduced by 15%, thereby negating the effect of increased numbers of workers outside, the results were still significant at $P = 0.015$ (one-tailed randomisation test, as before). This suggests that the increase (if any) in worker numbers outside the nest would not be enough to account for the increase in numbers of bouts.

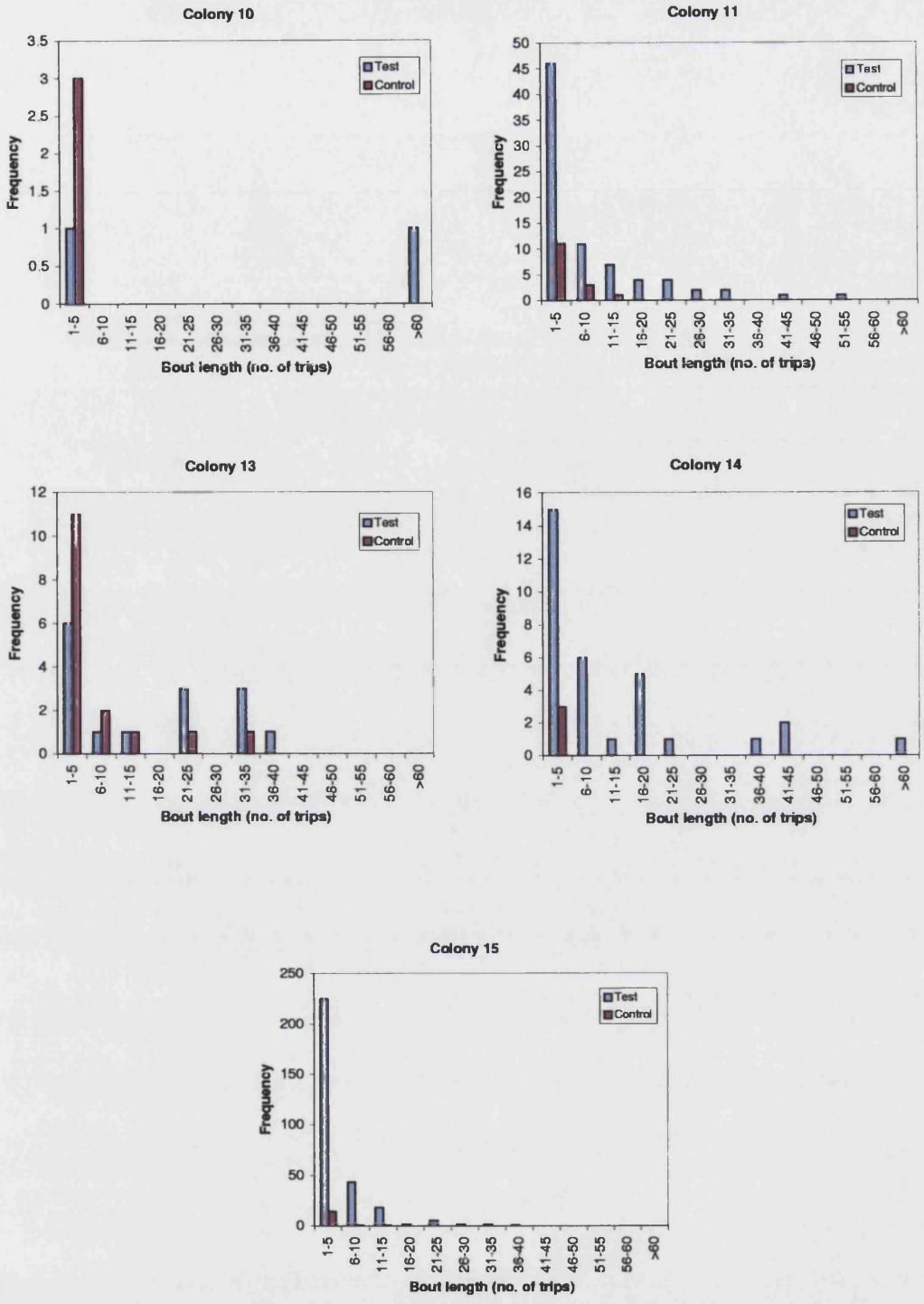


Figure 6.8: Distribution of bout lengths for each colony and treatment (pooling bouts from trials done with the same colony and treatment: so each bar represents the number of bouts from two trials, under test or under control conditions, that fall into the corresponding length class). Note that the scale of the vertical axis (frequency) varies between histograms.

	Treatment	
Colony	Test	Control
10	–	1.0
	34.5	2.0
11	7.42	1.0
	13.25	4.0
13	17.78	7.0
	12.83	1.0
14	24.0	–
	8.5	3.0
15	4.7	1.8
	4.1	3.4

Table 6.6: Mean number of events per bout in each experiment (– signifies that no bouts were observed).

6.3.3 Length of bouts

The lengths of all bouts observed are listed in Table 6.7. Mean bout lengths per experiment are summarised in Table 6.6 and the distribution of bout lengths for each colony/treatment combination (i.e. pooling the bouts observed in the two trials done for each combination) is illustrated in Figure 6.8.

ANOVA or non-parametric equivalents cannot be used to test whether bout lengths are longer under test conditions, for the same reasons as with the data on bout numbers. A randomisation test was therefore again used. Here, there is the important additional factor that the number of bouts per experiment varies. In consequence, to take a summary measurement (such as mean bout length) from each experiment and to test the summary values for departures from expectation is rather unsatisfactory, as some means summarise a single observation whereas others summarise around one hundred and fifty. Apart from this inconsistency, if more detailed data are available then using only the mean bout length from each experiment greatly reduces the power of the test. Randomisation testing, however, can take every observation into account.

A one-tailed randomisation test indicates that the increased length of bouts under test conditions is fairly significant ($P = 0.025$; see Section 6.3.5 for description of test).

Colony	Treatment, replicate	Bout lengths
10	Test 1	
	Test 2	68, 1
	Control 1	1
	Control 2	3, 1
11	Test 1	55, 44, 34, 30, 27, 18, 17, 16, 15, 15, 13, 12, 12, 12, 11, 10, 10, 10, 10, 9, 7, 7, 6, 6, 6, 5, 5, 5, 4, 4, 4, 3, 3, 3, 3, 3, 2, 2, 2, 2, 2, 2, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1
	Test 2	31, 25, 23, 22, 21, 17, 10, 3, 3, 2, 1, 1
	Control 1	1
	Control 2	14, 9, 6, 6, 5, 4, 2, 2, 2, 2, 1, 1, 1, 1
13	Test 1	35, 32, 32, 24, 24, 7, 3, 2, 1
	Test 2	38, 24, 11, 2, 1, 1
	Control 1	32, 25, 12, 7, 6, 2, 1, 1, 1, 1, 1, 1, 1
	Control 1	1, 1, 1
14	Test 1	116, 44, 40, 25, 17, 7, 5, 4, 3, 2, 1
	Test 2	41, 17, 17, 17, 16, 11, 10, 9, 8, 7, 6, 5, 4, 2, 2, 2, 1, 1, 1, 1, 1
	Control 1	
	Control 2	4, 3, 2
15	Test 1	31, 31, 28, 25, 23, 22, 21, 18, 18, 15, 13, 13, 13, 13, 12, 12, 11, 11, 11, 10, 10, 10, 9, 9, 9, 9, 8, 8, 8, 8, 7, 6, 6, 6, 6, 6, 6, 6, 5, 5, 5, 5, 5, 5, 5, 5, 4, 4, 4, 4, 4, 4, 4, 4, 4, 4, 4, 4, 4, 3, 3, 3, 3, 3, 3, 3, 3, 3, 3, 3, 2, 2, 2, 2, 2, 2, 2, 2, 2, 2, 2, 2, 2, 2, 2, 2, 2, 2, 2, 2, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1

Colony	Treatment	$\hat{p}$	G	P
10	Test	0.028	3.28	0.12
	Control	0.375	0.65	0.83
11	Test	0.107	24.9	0.31
	Control	0.208	5.58	0.66
13	Test	0.060	8.76	0.67
	Control	0.145	13.6	0.07
14	Test	0.067	23.6	0.11
	Control	0.25	2.69	0.21
15	Test	0.185	28.6	0.15
	Control	0.26	2.98	0.92

Table 6.8: Goodness of fit of bout lengths to the geometric distribution. Data pooled from both replicates under each colony/treatment combination. $\hat{p}$ is the maximum likelihood estimation of p, the giving-up probability at the end of each fetching trip. G is the G-statistic for goodness of fit (Sokal & Rohlf, 1995) to the corresponding geometric distribution. P is the significance of the G-statistic, determined as detailed in Section 6.3.5.

6.3.4 Distribution of bout lengths

It can be seen from Table 6.7 and Figure 6.8 that the distribution of bout lengths is strongly skewed, with short bouts being very common and longer bouts being progressively rarer. This suggests that there might be an approximately constant probability of giving up a bout at the end of each fetching trip within it. If so, bout lengths would approximate the geometric distribution. The geometric distribution is the distribution of X being the number of trials before the first 'success' in a sequence of independent trials each having probability p of 'success' (Johnson & Kotz, 1969, p. 123). 'Success' may actually mean failure, or any event of interest; here it denotes the end of a bout.

Using G-tests (Sokal & Rohlf, 1995), the bout length data were found to be reasonably consistent with the geometric distribution; Table 6.8 gives $\hat{p}$, G and significance values. Further details of tests are given in the following section.

6.3.5 Statistical tests

Randomisation tests

Since randomisation tests are not altogether commonplace, a brief description of how they operate is in order. The reasoning behind randomisation tests is as follows. Since the null hypothesis is that the treatments applied have no effect on the results observed, it follows that under the null hypothesis a result observed under one particular treatment was just as likely to have occurred under any of the other treatments. That means that a statistic (such as t or F) computed from the observed data should not be any more likely to have an extreme value than the same statistic computed after shuffling the observed results at random between the different treatments—if the null hypothesis is true. Furthermore, if many such randomly shuffled data sets are produced and the statistic is computed for each one, the proportion that are as extreme as that calculated from the real data, or more extreme than it, approximates the probability that the observed results could have been obtained under the null hypothesis. For a data set, permuted at random, only rarely to give a value of the statistic as extreme as that obtained from the original data, is unlikely to occur under the null hypothesis. Indeed there is a probability x/N that the set of data sets comprising the original data and $N - 1$ random permutations of it will contain x members that give a statistic as extreme as or more extreme than that computed from the original data (Edgington, 1980; Manly, 1991).

Randomisation tests do not make assumptions about the type of distribution the results are drawn from. This is because they do not make any statement about the population from which the results were drawn, but only about the results actually obtained; inferences about the population must be made by non-statistical means (Edgington, 1980; Manly, 1991). Another advantage is that they can be carried out on results not merely whose distribution but whose very format does not fit standard tests.

Numbers outside the nest

ANOVA was carried out using the General Linear Model in Minitab Release 12.1 (Minitab Inc., 3081 Enterprise Drive, State College, PA 16801–3008 USA).

The null hypothesis for the randomisation test is:

> **H_0: the treatment used does not affect the number of workers outside the nest for a given colony at a given time within the experiment.**

Since there seems to be an effect both of colony and of the time within the experiment at which an observation was made, the method of Edgington (1980) was used, and each observation was randomly shuffled only with other observations from the same colony at the same time, rather than with observations across all colonies and times. The table in the following section shows a hypothetical example of such a randomisation in the simpler case where there is only one observation per colony.

The test statistic used was simply the sum of numbers outside for all experiments under test conditions at all times. This is a one-tailed test statistic. In none of 999 999 randomly permuted data sets[1] was this value as large as the value of 13631 actually observed. (It may be surprising that the result is so highly significant, when visual inspection of the graphs on page 126 does not suggest any effect at all, but the frequency distribution of the randomised statistics shown in Figure 6.9 confirms its extreme rareness under randomisation of the sample.) The probability of this occurring under the null hypothesis is 0.000001.

I also wanted to compare the size of the treatment effect on numbers of workers outside the nest with data on the amount of fetching. Confidence limits for the size of the treatment effect in those experiments were therefore calculated. The method used is based on the randomisation test which it has already been shown may be flawed; its results cannot therefore be trusted but it is nonetheless interesting to perform the calculation. The 95% confidence limits for the treatment effect, when calculated as described below, were 1.01 and 2.95. That is, test conditions increased the number of workers outside the nest by between about one and three workers compared to control conditions. The experiments used to calculate these confidence limits were the first two test and the first two control experiments for colonies 10, 11, 13, 14 and 15, which are the ones for which fetching data are available. No fetching occurred in colony 12, and it was excluded from this analysis.

[1] Eight experiments were done on each colony, so for any given time and colony there are eight observations, which can be randomised 8! ways. Twenty-four observations were taken during each experiment, and there were 6 colonies. Thus there are $(8!)^{24\times6} \approx 1.48 \times 10^{1918}$ possible permutations.

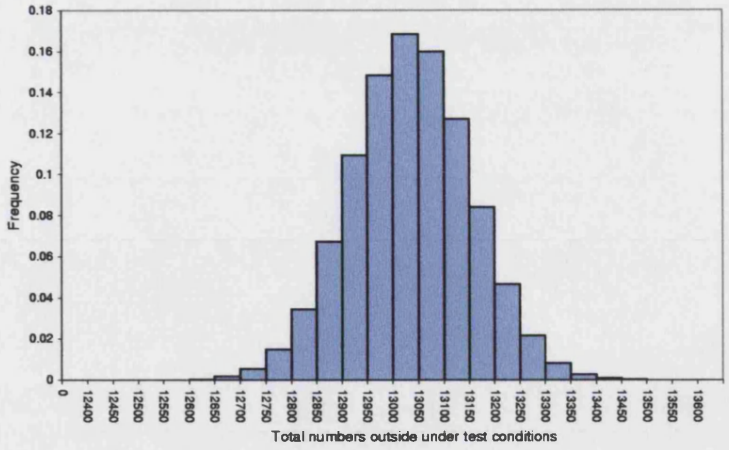


Figure 6.9: Distribution of the test statistic for numbers of workers outside the nest. The distribution shown is that of, for randomised data, the sum of all counts of numbers outside under test conditions. The value obtained for this statistic for the real data was 13631, whilst the equivalent sum for counts under control conditions was 12439 for the real data.

The method used to calculate confidence limits is given by Manly (1991). The two values were found (by iterative sampling) which, when subtracted from every observation under test conditions, were the exact size necessary to give a significant result at the 0.05 level on a two-tailed randomisation test (test statistic was the absolute difference between the sums of test and control observations). The justification for this technique (Manly, 1991, p. 19) is simple. Assume that treatment causes a fixed increase μ_D in observations under test conditions. Whatever the true value is of this increase, if it were subtracted from every test observation before performing the test, the probability of getting a 5% significant result would be 0.05. Since, if we subtract the true value of μ_D, we can be 95% confident that a randomisation test will not give a significant result at the 5% level, we can be 95% confident that the true value of μ_D lies within the range of values (empirically determined) for which a non-significant randomisation test result is obtained at the 5% level.

Number of bouts

The null hypothesis for this test is:

> **H_0: the treatment used does not affect the number of bouts a colony performs.**

As with the previous test, since there appears to be a colony effect (and the null hypothesis is only that *for each colony* the same number of bouts can be expected regardless of treatment), each observation was randomly shuffled only with other observations from the same colony, rather than with observations across all colonies. To illustrate, the following hypothetical data set from two colonies (letters A, B etc. representing individual observations)

Colony	Test	Control
α	A	C
	B	D
β	W	Y
	X	Z

might be randomly permuted to

Colony	Test	Control
α	B	A
	C	D
β	Y	W
	Z	X

but not to

Colony	Test	Control
α	A	D
	X	Y
β	C	B
	W	Z

The test statistic used was the sum of observations in the "Test" column—the simplest useful statistic. This statistic gives a one-tailed test.

The observations in Table 6.5 can be permuted a total of 7 962 624 ways.[2] Of 99 999 permutations generated pseudorandomly with replacement from that data, 812 had at

[2]Four observations per colony gives $4! = 24$ permutations per colony; with five colonies, there are $24^5 = 7962624$ permutations overall.

least as large a sum of observations in the "Test" column as the real data; consequently the probability of the observed results occurring under the null hypothesis can be estimated as $P = 0.008$.

Length of bouts

The test for bout length was slightly more complicated, since the number of observations in each cell was variable. Observations of individual bout lengths were shuffled, rather than the mean bout length per experiment, as this increases the power of the test. As with the test of bout numbers, and for the same reasons, data were only shuffled amongst the observations for each colony, rather than across all colonies; and again the simplest way to demonstrate what was done is by illustration. This time, only a single-colony example is shown. The data set

	Exp't	Bout lengths	Mean bout length	Exp't	Bout lengths	Mean bout length
Colony α	First test	A, B, C, D, E	$\frac{A+B+C+D+E}{5}$	First control	J	J
	Second test	F, G, H	$\frac{F+G+H}{3}$	Second control	K, L	$\frac{K+L}{2}$

might be permuted as follows

	Exp't	Bout lengths	Mean bout length	Exp't	Bout lengths	Mean bout length
Colony α	First test	B, E, G, J, K	$\frac{B+E+G+J+K}{5}$	First control	D	D
	Second test	A, C, L	$\frac{A+C+L}{3}$	Second control	F, H	$\frac{F+H}{2}$

The statistic used to determine P was calculated by summing the bout lengths for all bouts in all trials under "Test" conditions (the fourth column in the table above).

Note that whilst assigning bout lengths from a colony at random amongst all the experiments done on that colony, the number of bouts in each experiment is kept the same. Retaining the structure of the data in this way prevents the inequalities in that structure from biasing the significance value found. For instance, one experiment may contain a large number of observations including one or two extremely large values which might be seen as outliers that bias the sum of bout lengths for that experiment. Suppose that these large values were present in a test trial but absent from a control trial, not because of a treatment effect, but simply because far fewer bouts were observed in the control experiment and these bouts happened by chance to be the common, short ones rather than the rare, long ones.[3] By retaining the structure of the data when permuting them at random, the control experiment continues to contain fewer observations, and so it remains unlikely that any of these observations will be extreme ones. If the null hypothesis is true, the lengths of the bouts observed for a colony (under either treatment) can be considered as samples drawn from the same distribution. Thus, a control experiment had as much chance (albeit a small chance) of producing extreme bout lengths in the real data as it does in the permuted data sets. Similarly—if the null hypothesis is true—extreme values have the same elevated probability of being found among the test experiments after random shuffling as they did of appearing there in the first place.

By contrast, if it transpires that randomly shuffled data sets rarely have means of bout lengths for test experiments as high as the real data, we can conclude that the data were unlikely to have been obtained under the null hypothesis.

The data in Table 6.7 have 2.44×10^{869} possible permutations.[4] 99 999 data sets were generated by pseudorandom permutation with replacement; of these 2507 were found where the sum of the mean bout lengths for all test experiments was as high as or higher than the value (2713) calculated for the real data, from which the probability that the null hypothesis holds for the data obtained can be estimated as $P = 0.025$.

Distribution of bout lengths

The maximum likelihood estimator for the geometric distribution is

[3] Bout lengths appear to approximate the geometric distribution (see Section 6.3.4). This means that short bouts are common, and longer ones progressively more rare.

[4] Five bouts were observed from colony 10, 93 from colony 11, 31 from colony 13, 35 from colony 14 and 314 from colony 15. Thus the number of possible permutations for each colony are 5!, 93!, 31!, 35! and 314! respectively, and the total number of permutations is $5! \times 93! \times 31! \times 35! \times 314! = 2.44 \times 10^{869}$.

	Treatment	
Colony	Test	Control
10	0.0	0.0
	0.248	0.012
11	1.744	0.0
	0.585	0.256
13	0.566	0.341
	0.301	0.0
14	1.034	0.0
	0.713	0.017
15	1.892	0.067
	2.382	0.118

Table 6.9: Mean number of workers fetching at one time.

$$\hat{p} = \frac{1}{1 + \bar{X}}$$

where $\bar{X}$ is the mean of the observations (Hogg & Tanis, 1983). The G-statistic is calculated as

$$G = 2 \sum_{i=1}^{a} f_i \ln \left(\frac{f_i}{\hat{f}_i} \right)$$

where f_i are observed and $\hat{f}_i$ expected frequencies in each of a classes. The expected frequences are calculated from the geometric distribution

$$\mathbf{X} = p(1-p)^0,\ p(1-p)^1,\ p(1-p)^2,\ \ldots,$$

$p = \hat{p}$. G is generally held to approximate the χ^2 distribution, but because of the small frequency class sizes in these data, the assumption is unreliable here (Sokal & Rohlf, 1995, chapter 17). Instead, significance was estimated by Monte Carlo simulation: 10000 samples of the same size as the observed data were taken from the geometric distribution with $p = \hat{p}$ and G was calculated for each, P being given by the proportion that had values of G at least as extreme as the real data.

6.4 Discussion

The results provide three main findings:

1. a possible but quite small increase in the numbers of workers outside the nest when a wall is absent;
2. an increase in the number of bouts of fetching;
3. an increase in the number of fetching trips per bout ('bout length').

6.4.1 Increased numbers of workers outside the nest

If indeed there is an effect (and the results obtained are not clear on this point) one possible explanation is that, rather than an increase occurring because more workers were leaving the nest due to the absence of wall, workers were just as likely to leave the nest but then spent longer outside because they began bouts of fetching. Judging from their behaviour after finishing bouts, fetchers come from a population of workers that spend significant portions of their time both inside and outside the nest, and probably exit the nest for stretches of several minutes. When they are induced to perform bouts of fetching, however, they may be outside for longer stretches. In this way, an increased probability of responding to the pile of building material, and of continuing a fetching bout once begun, might lead to more individuals being observed outside the nest, even without the absence of wall directly leading to an increased probability for workers to exit the nest.

It was possible, from the data gathered during video analysis, to extract information about the numbers of individuals actually engaged in fetching at any one time, and the mean difference in the numbers fetching between test and control conditions for these experiments was 0.87. (Table 6.9 gives the mean numbers engaged in fetching at one time for each experiment.) Although smaller than the observed treatment effect, and furthermore outside the 95% confidence limits of 1.01 to 2.95 calculated for those experiments where fetching data is available, these confidence limits cannot be trusted any more than the randomisation test with which they are derived.

If the absence of a wall caused more workers to leave the nest, the size of the increase

is yet quite small—at most about 15%. It may have happened in two ways. There could be a small caste of fetching-specialists, who have a greatly increased probability of exiting the nest when its wall is incomplete. Alternatively, the absence of wall could lead to a generalised but small increase among workers in the probability of leaving the nest. One way in which this might happen is if the absence of wall interacted with worker's movement rules so as to make exit more likely, rather than by workers detecting the absence of wall and changing their movement pattern in response. For instance, if workers have a tendency for edge following behaviour, they would exit the nest with higher frequency when less of the wall is present. This is an appealing idea because the wall would be regulating itself through its effects on worker behaviour, rather than the workers' behaviour containing an element to monitor wall state. As it relies less on sophistication in the active agents carrying out the process than on the natural tendency of the system, such a mechanism might be more robust. Further experiments using marked individuals would help establish whether the extra individuals that are found outside the nest are a small caste of specialists or a selection from a larger group. If a caste of specialists is responsible, it seems likely that they would be actively monitoring the state of the wall. If the effect is a generalised one in the majority of outside-nest workers, more subtle manipulations would be necessary to determine whether there was active monitoring or merely passive response to the state of the wall.

6.4.2 More bouts

The results showed that there was an increase in the number of bouts over and above that which could be explained by any increase in the number of workers outside the nest. If we assume that the probability of encountering the pile of building material is proportional to the amount of time spent outside, which seems reasonable, then the increase in the number of bouts must be caused by workers having an increased probability of responding to the pile of building material upon encountering it. Thus the workers' behaviour is affected by their previous experience. It could be said that the stimulus for performing the fetching task consists in two parts which are spatially and temporally separate, and the response is only seen once the second part has been encountered. Another way to consider it is that the response to the pile of building material is context-dependent (Blanchard, 1997), but the context on which it depends is not the ant's immediate surroundings at the point the differential response occurs, but rather its circumstances on a prior occasion in a different place. This can hardly be the

only case in which such an effect occurs, and it underlines the difficulties in analysing social insect behaviour discussed by Blanchard (1997) and Bourke & Franks (1995, Ch. 12). It would be particularly interesting to know whether the extra workers outside the nest are composed of a small group of fetching specialists or not. If so, then one only has to posit an ability of workers to store information related to their speciality. If not, then it suggests that workers may remember aspects of their environment that do not relate to a current task specialism, opening the possibility that they may store many parameters and therefore have a more complete picture of the state of the colony and nest (at least in small colonies) than they are commonly credited with, each datum being stored merely against the possibility of its being useful at some future time.

One possibility that the results given do not rule out is that it is wrong to assume a linear relationship between number of workers outside the nest and rate of encounters with the pile of building material. It could be wrong if workers that start bouts do not previously exhibit the same pattern of movement as other workers outside the nest. That is, workers that are about to start a bout of fetching might travel more directly to the pile of building material than others, if they already know where it is. Essentially this amounts to a distinction over where the bout begins, and hence where the point of decision is. It is possible that the decision to start a bout occurs entirely within the nest, and is followed by a direct journey to the building material, so a large increase in bouts goes with a small increase in numbers outside the nest and yet the probability that those workers who encounter building material by chance (whilst outside the nest) will respond to it is no higher.

However, this possibility is unlikely for two reasons. Firstly, to produce such an effect, most of the workers that fetch material would have to be ones that take a decision to fetch whilst within the nest and proceed directly to the pile of building material—yet they would need previous knowledge of the pile's location. Thus the effect would not materialise until some way into the experiments. Secondly, whilst analysing the videos, those workers that began bouts did not appear to have issued directly from the nest but rather to have been wandering outside it. The workers outside the nest have two quite distinct patterns of movement, according to whether they are engaged in a fetching bout. Whilst not fetching, they wander slowly and haphazardly, with much turning and a strong edge-following tendency. When fetching, they move directly and purposefully between the pile of building material and the nest (in either direction), and if they mistake the trajectory and miss their destination they perform an area limited search until they either find it and recommence the behaviour, or give up and wander

haphazardly. These two behaviour patterns are quite stereotyped and almost instantly recognisable.

6.4.3 More fetching trips per bout

As just mentioned, it is clear when a worker re-exits the nest after depositing an item of building material whether it has the intention of returning directly to collect more. If it does not make directly for the pile of building material, then instead it wanders haphazardly either inside the nest or outside it. It is therefore fairly clear that a decision point occurs immediately after an item of building material has been dropped inside the nest. At this point, information is available about the state of the wall which could be used to influence the decision, and so it is naturally a convenient point at which to regulate the fetching behaviour. The results show that this does indeed happen. It has already been noted that workers bringing building material into the nest tend to drop it deeper inside the nest than the area in which the wall ultimately forms. One quantity that could inform the decision is therefore the amount of obstruction the worker encounters in trying to re-enter, or the amount of time that it takes to do so. It was noticed whilst analysing the experiments described in the previous chapter that these workers take considerably longer to enter and re-exit the nest when the wall approaches completion, as the number of ways through the material deposited becomes fewer and they have to search for a passage by trial and error.

6.4.4 Summary

In summary, the results show that the nest wall is regulated as follows. Possibly there is a slight increase in numbers outside the nest triggered by absence of wall, though if the effect is real its size is relatively negligible. It might be explained either by a small group of workers becoming much more likely to leave the nest, or by a small increase in the probability of exiting among a large group. An increased probability of responding to building material amongst some or all of the workers outside the nest was clearly established, and on returning to the nest with building material there is an increased probability of repeating the behaviour, leading to longer bouts of fetching. Thus at least two and possibly all three of the regulatory points suggested in the Introduction to this chapter have some involvement.

6.4.5 Regulation of fetching: comparison with other tasks having similar features

How does the picture built up here of regulation of the fetching task compare with what is known about the regulation of other tasks that have similar features?

The principal features of the fetching task are that individuals work independently, that the task can reach completion (i.e. that demand for it can be satisfied, at least temporarily), and that the source and sink of task material are spatially separate. I mentioned in the Introduction to this chapter some tasks that share at least two of these features. Here I discuss what is known about their regulation.

Comb construction by honey bees has the features that the task can be temporarily fulfilled and that workers work independently (at least, they do not communicate directly concerning the task; Pratt, 1998 suggests that indirect communication occurs through the medium of the comb). However, the task is more complicated in that there are two levels of decision: firstly as to whether to build comb at all (Pratt, 1999), into which the need for food storage space has an input, and secondly as to whether to build worker or drone comb (Pratt, 1998). Whilst the bees appear to be indifferent as to which kind of comb is used for food storage (S. C. Pratt, personal communication; Winston, 1987), the decision to build drone comb appears to be subject to a negative feedback mediated by the workers such that existing empty drone comb inhibits the construction of more drone comb. Exactly how this negative feedback operates, in terms of individual workers' behavioural rules, is not clear.

Nest construction in wasps, while ostensibly similar to comb construction in honey bees, has the extra feature that the materials used in construction (wood pulp and water) have to be foraged, which adds an extra degree of similarity to the fetching of building material in *L. albipennis*. Jeanne (1986b) found in *Polybia occidentalis* that three distinct tasks are involved in construction, namely foraging for wood pulp, foraging for water, and combination of wood pulp and water into new nest structure. These tasks are carried out by different workers, with the first two groups transferring material to the builders, but workers are more likely to switch between the activities in smaller colonies. This fact suggests that queueing delays in waiting to transfer material to recipients, or to receive it from foragers, might be used to regulate the level of activity in the different tasks by inducing workers to switch (Jeanne, 1986b), in a manner

reminiscent of the foraging-for-work hypothesis (Tofts & Franks, 1992; Tofts, 1993). Queueing delays have certainly been shown to be involved in regulating nectar foraging and receiving efforts in honeybees (Seeley, 1995; Ratnieks & Anderson, 1999b; Anderson & Ratnieks, 1999b). Here, however, rather than inducing workers engaged in foraging or in receiving nectar to switch to each others' tasks, the extent of queueing delays induces returning foragers to perform either a waggle dance (stimulating extra foragers) or a tremble dance (stimulating extra receivers), or, intermediately, neither (Seeley, 1995).

Both nest construction in wasps and nectar foraging in honey bees involve direct transfer of material from foragers to recipients. It is the direct transfer that makes information available to the workers that can be used to regulate their performance of the task (and at the same time can introduce inefficiencies; Anderson & Ratnieks, 1999a). Building material is transferred indirectly in *L. albipennis*, eliminating the potential for such a mechanism. It can be seen that this difference is fundamental for the regulation of the task. Another important difference in foraging for food materials is that effort expended by the colony on the task is governed more by the availability and cost-effectiveness of supplies than by demand, if (as in honey bees) surplus food can be stored. By contrast, in the task examined in this chapter, there is no point searching for additional material if the wall is already complete.

A review of foraging tasks and other material-handling tasks in which the handling process is partitioned, with examples of both direct and indirect transfers, is provided by Ratnieks & Anderson (1999a) (see also Anderson & Ratnieks, 2000). Leafcutter ant foraging is one significant case in which indirect transfer occurs. However, whilst the examples of this phenomenon are well documented, the regulation of the process does not appear to have been studied.

In summary, the picture from the literature is that, where tasks involve indirect transfer of material, the size of the cache of material or cues associated therewith are used to regulate performance of the task. The results presented in this chapter indicate that fetching of wall material in *L. albipennis* fits in to this picture. However, there is still scope for further experimentation to explore how it is determined which individuals respond out of all those that have access to the relevant cues, not only in this task but in other examples of indirect transfer.

Chapter 7

Discussion

7.1 Summary of thesis

7.1.1 Evidence suggests a distinction between task allocation occurring within and between roles, and between small and large groups

In Chapter 2, I argued that available empirical evidence points toward some fundamental differences between task allocation that occurs in the short term, over time scales of minutes to hours, and that which occurs over time scales of days or longer. I proposed that most social insect species fit a pattern of two to four roles, characterised by increasing risk, through which workers tend to progress over the course of their lives, and that workers may switch on shorter time scales between the tasks comprising one role. I also contended that there are strong reasons why task allocation in small groups has to meet different requirements from task allocation in large groups, and therefore can be expected to employ different mechanisms.

7.1.2 Between-role task allocation in small groups is least well understood

None of these classes of task allocation are genuinely well understood at present. Neither individual behavioural rules nor the relationship between those rules and the group dynamics have been thoroughly mapped for any species. For some species, task allocation patterns are very well documented, but most of the evidence is descriptive and establishes what phenomena occur rather than endeavouring to explain them. There are some exceptions, where the mechanisms of task allocation are in the process of being teased apart by 'sociotomy' techniques, notably the honey bee and the ant species *Leptothorax unifasciatus* and *L. albipennis*. Here, experiments are asking the questions that will lead to a fuller understanding of task allocation mechanisms. Manipulating the colony age structure provides a means to control the experiences of individual workers, and thence by observing both individual and collective responses, the behavioural rules in operation are revealed little by little. Particularly in honey bees, some aspects are already understood (for instance, it has been demonstrated that accelerated or retarded behavioural development is caused by abnormally low or high numbers, respectively, of older workers, but not exactly how the effect is mediated) and there is every reason to expect that the system will be well characterised within the near future.

However, the areas where most progress has been made have concerned long-term, that is between-role, task allocation. Rather little is known, by contrast, about short-term task allocation. That is, numerous cases have been demonstrated of flexibility in short-term task allocation, but nothing is known of the mechanisms underlying most of those cases. A notable exception is the receipt of foraged nectar in the honey bee, where the relationships between foraging success, queuing time for nectar offloading, the type of signal produced by foragers, and the responses of other bees, have been beautifully deciphered (reviewed in Seeley, 1995). However, the honey bee lives in large colonies. Chapter 2 explained why the same mechanisms might not work in a small group.

It is also significant that the previous example involves foraging. Indeed, in general the mechanisms governing foraging have been subjected to more study than those governing within-nest task allocation, presumably because foraging is easier to study since it takes place in the open air. Much study of foraging has investigated the dynamics

of foraging pheromone trails and the constraints on choice behaviour between different resources (Deneubourg & Goss, 1989; Detrain *et al.*, 1999; Couzin, 1999), and it is arguable whether this constitutes task allocation. Some decisions within foraging, though, can reasonably be taken as task allocation decisions, as when there is a choice between different forage materials. Studies that have looked explicitly at short-term task allocation (such as that of Gordon, 1989), if not being restricted to foraging, have at least concerned only outside-nest tasks.

One of the conclusions resulting from the work in this thesis, however, is that there are likely to be important differences between task allocation inside the nest and outside it. The reason is that (at an approximation) social insects do not control the structure of the environment outside the nest, whereas within it they do. Chapter 4 showed that differences in spatial structure can have some quite profound effects on the operation of task allocation. Therefore, within the nest, arranging the environment is one of the tools available to social insects for ensuring an orderly and adaptable division of labour, whilst outside it different tactics may be needed. It follows that inferences made from outside-nest behaviour cannot necessarily be transferred inside the nest.

In summary, then, there is a lack of evidence concerning short-term task allocation in small groups, particularly within the nest. It is interesting that this is precisely the category which might be expected to have most parallels with multi-agent systems engineered by humans (see Chapter 1).

7.1.3 Summary of achievements presented in these pages

The work presented here was therefore undertaken as one step towards ameliorating that lack. The modelling work was aimed at understanding better how short-term task allocation might work, both within and without the nest, and at making predictions that would allow testing for the presence of one particular algorithm. That has been largely achieved. The goal of the experimental chapters was to elucidate the regulation of a specific task in a particular species, namely the fetching of wall material in *L. albipennis*. Here, whilst a full description of the task's regulation was not obtained, some significant results were found which together build up a partial picture and suggest some good possibilities for further work (discussed below).

7.2 Problems encountered here reflect general problems in task allocation studies

It is instructive to consider the flaws in the work presented here, since although efforts were made to avoid in particular the failings of some previous modelling work (see Chapter 2), the problems encountered herein are a microcosm of those facing studies of social insect task allocation in general.

In this section, therefore, I discuss some shortcomings that have come to light in the present study, and show how they reflect similar tendencies in the field as a whole. In section 7.3, these issues are developed firstly into suggested extensions to the current work, and secondly into recommendations for task allocation studies generally.

7.2.1 Integration of modelling and experimental work

The first improvement that I would wish to make to this work would be to integrate the experimental work more closely with the modelling work. Both seek to explore similar themes, involving responses to changing stimuli and the involvement of reinforcement, but there is no formal integration in the sense that the experiments were not designed to test the models.

In fact, with experiments and modelling proceeding in parallel as was the case, it would have been difficult to integrate them any further without going into a second iteration of the process whereby each could have been directed by the other. The experiments sought to establish a basic understanding of the task in question, and such a basic understanding is necessary before one can begin to devise experiments that would test a given model.

The results found so far actually tend to indicate some incompatibility between the model of propensity reinforcement and the task of fetching wall material in *L. albipennis*: the model is not quite adapted to describing that particular task, or alternatively the task is not quite suitable as a test case for that particular model. However, without the work that has been done, the insights would not have been reached which lead to that conclusion. Furthermore, it is precisely the realisation of this gap that leads to

interesting possibilities for future work (see below).

What is incompatible between the two? Potentially, although they were not aimed directly at testing the propensity reinforcement model, the experimental results obtained could rule it out in the simple form developed herein.

Over the time scale of a bout of fetching, a worker is returning to the source of building material, whose location it knows. By contrast, in the model workers have no knowledge of the whereabouts of task items. There will therefore be biases in encounter patterns in the real world which do not exist in the model.

Over the time scale of a single wall building session (as provoked experimentally by emigration), fetching behaviour seems to occur as a probabilistic response to building material among some subset of the workers; it is then followed by repeated fetches whose number is approximately geometrically distributed. This suggests a constant per-trip giving up probability, which may not be consistent with the pattern of giving up that occurs in the propensity reinforcement model.

Over the longer term, between occasions on which the wall is rebuilt, propensity reinforcement cannot be taking place in the manner modelled in this thesis. There is no encounter with the task stimulus between one wall building session and the next, and so under the present model propensities for fetching would fall to zero during that time. However, this does not rule out some other reinforcement mechanism lacking the effect that in the absence of a task, probability of responding to it becomes very low or zero. As well as propensity reinforcement, this could include a threshold mechanism like that of Bonabeau *et al.* (1998a). In fact, that model has already been extended by Theraulaz *et al.* (1998) to include a reinforcement effect, but the effect of response probability falling away in the absence of a task is similarly present. A mechanism that did not have it would need an alternative feature for ensuring that workers did not end up becoming sensitive to all types of task, and it is not immediately obvious how that might be arranged.

A lack of integration between models and experiments is, unfortunately, common in the literature. Indeed it is rare to find both models and experiments presented together. As observed in Chapter 2, the standard of modelling has not always been satisfactory, and many models that have been published do not take sufficient steps to provide means by which they might be tested experimentally. Those that do seem not to have

stimulated much actual effort to test them.[1] Even the more serious contenders, which are probably response thresholds and foraging-for-work (FFW), have some significant problems. In the case of FFW, the problem is with testability: attempts have been made to test FFW against an alternative of age-based polyethism (Calderone, 1995) but have only succeeded in demonstrating that age is a factor. Since Tofts & Franks (1992) explicitly stated that they expected FFW to operate in concert with other factors including age and genotype, this remains inconclusive. In the case of response thresholds, there is some evidence supporting the idea of thresholds (Bonabeau *et al.*, 1998a), but even if response thresholds do model well the behaviour of real social insects, the important questions are less to do with what happens if there is such-and-such a colony profile of thresholds, as with how the colony profile of thresholds comes about and how it responds to circumstances. This latter question does not appear to have been addressed.

7.2.2 Models: conflating abundance with priority, and combining models of local and global stimuli

An interesting flaw in the propensity reinforcement model presented in Chapters 3 and 4 is that it implicitly assumes that the abundance of a task is concomitant with its priority. This is also a feature of some of the models reviewed in Chapter 2, notably that of Pacala *et al.* (1996), and to some extent of response thresholds (Bonabeau *et al.*, 1996, 1998a).[2] The tendency of the propensity reinforcement model is to equilibrate task items of all types at appoximately the same density. The principle on which its rule for individual behaviour is built is that, if the individual meets a particular type of item more often, it should become more likely to perform it.

Many tasks do fit this assumption, where the basic goal of an algorithm is to maintain the task demand within certain bounds: if it sinks too low, effort will be more profitably spent elsewhere, and if it rises too high, effort spent elsewhere is better diverted to it.

[1]The exception is the study of foraging, where integration between models and experiments, using experimental systems such as binary choice pathways or choice experiments between pairs of resources, has had impressive results (reviewed in Detrain *et al.*, 1999).

[2]Response thresholds actually assume that there is some level of *stimulus*, which makes task performance more likely the higher it is. Although it is easiest to imagine this stimulus as being the abundance of some factor, in principle it could equally be its absence. Thus response thresholds do not assume a relationship between abundance and priority, but since they do not model the relationship between colony conditions and the stimulus level perceived by workers at all, they cannot assume some other more realistic relationship either.

Examples (see e.g. Hölldobler & Wilson, 1990; Winston, 1987; Seeley, 1995) could include hygienic behaviour (self- and allo-grooming, removal of detritus and corpses), receipt of foraged material, larval care and feeding, and construction of brood cells (for wasps and bees) or galleries (for ants and termites).

However, there are also cases that do not fit this pattern. Some tasks may be more important the rarer their associated stimulus becomes; others may always take priority over other tasks. The most obvious example of the first is foraging. The rarer food becomes, the more valuable it is and therefore the greater the importance of harvesting it. For the second, colony defence provides a good example: if the nest is opened, it becomes more important to carry larvae to safety than to feed them, however hungry they are.

An additional flaw in all the models examined in Chapter 2 (as well as the one presented in this thesis) is that they limit themselves to modelling stimuli either as multifarious, locally encountered items or as single, global variables. In reality, the stimuli in social insect nests are a mixture of the global, the strictly local, and the intermediate. Whilst one can model only global or only local stimuli, and perhaps obtain good agreement between the model and empirical data, one cannot then account for what happens when a worker faces a decision between responding to a local stimulus and responding to a global one—something that probably happens frequently.

7.2.3 No work on within-nest tasks

The experimental work in this thesis examined a task that takes place largely outside the nest. As remarked above, the most serious gaps are in our understanding of task allocation within the nest. This is one area that I would particularly like to see explored in future. There is, unfortunately, a very good reason why it has been little explored in the past, which will probably persist in making within-nest task allocation less studied than other subjects, which is the difficulty of performing manipulations within the nest without causing so much disturbance as to disrupt entirely the patterns one seeks to examine.

Work on between-role task allocation has been more successful in this respect, because it is possible to explore the effect of the colony's age structure (an critical parameter, even in FFW where there is no direct dependence of task choice on individual age)

by artificially manipulating the composition of the workers. Although, clearly, such manipulations cannot be carried out without causing disturbance, the time scale of the disturbance is shorter than that of the effects being studied, and so the technique is practicable.

For within-role task allocation, age is probably not an important factor since the allocation is occurring in parallel between workers of the same role (which will often be the same age cohort), and furthermore the time scale of allocation and switching is much shorter, so that disturbances will have a correspondingly more serious effect on the establishment of normal task allocation patterns.

7.3 Problems encountered here supply directions for further work

There is considerable potential for *rapprochement* between the two threads of work reported here. The suggestions for further studies are borne out of the gaps outlined immediately above. Some more general recommendations also emerge from the issues raised.

7.3.1 Extensions to the work presented here

The first priority is to devise models that are attuned to the more detailed information now available about the task of fetching wall material in *L. albipennis*, and to devise experiments that can test predictions of those models. In other words, the cycle of modelling and experimentation (Camazine *et al.*, in press) needs to carry out a second iteration.

Models need not be mathematical models or simulations, in the normal sense of the word; any hypothesis from which testable predictions can be deduced is a model (Franks *et al.*, 1997). The principal unanswered question is how large the pool of workers is from which fetchers are drawn. To this one might add a desire to know by what means workers join (and indeed leave) the pool.

For determining the size of the pool of fetchers, the approach used in Chapter 5 should in principle be effective. The reason that those experiments did not produce a full answer is that effective identification of individuals was not achievable on the equipment available at the time. Since then, mass market digital video recording equipment has become available at similar prices to those previously applying to Super-VHS analogue machines. This equipment has sufficiently good resolution (particularly colour resolution) to enable identification of paint-marked workers when focused on a sufficiently small area of around 4cm × 5cm (Pratt & Mallon, in preparation). By placing a source of building material between four and five centimetres from the nest entrance and filming the area encompassing the two, it would be possible to identify all fetchers. (The reason for filming the entire arena in Chapter 5 was so that individuals identified with the pointer would remain in view, allowing them to be tracked from fetching to identification. It would not be necessary to film the whole arena if paint marks were distinguishable when playing back the videotape.)

Determining how a worker becomes a member of the pool would be a more interesting and a more challenging question. Suppose that the size of the pool had been found and was quite small—perhaps around five or less. Then it would be possible to carry out removal experiments, by identifying the members of the pool over the course of two or three wall building occasions (provoked by emigration). Upon their removal from the colony, further emigrations could be performed and the question asked: are the fetchers replaced by other individuals? The dynamics of replacement would provide the basis for developing models more closely attuned to the task. At one extreme, if no replacement occurs it implies that a propensity for the fetching task is predetermined. On the other hand, if replacement does occur then further questions could be asked:

- How does it occur?
- What prevents it occurring while adequate fetchers are already in place?
- From what group are the new fetchers drawn?
- By what criteria do they change from their previous status to being fetchers?

Another way to approach the question of how fetchers become fetchers is to look at what tasks they perform when wall is not required to be built. Are they foragers or inside-nest workers? Do they remain idle, or are they 'elites', working at above average levels on other tasks also? Answering these questions would require a long-term

study of the behaviours of the workers, perhaps using a photography technique like that of Sendova-Franks & Franks (1993, 1994, 1995) and Backen *et al.* (2000). Elucidating the details of a single task might not justify the investment of time and resources that such an approach would require, but it could form part of a broader investigation into within-role task allocation. Blanchard (1997) proposes the use of a computer image analysis system to reduce the data gathering load involved in such a process. It is not certain that either technique is satisfactory for detailed investigation of behaviour at present. Photographs being necessarily still, one is confined to defining task in terms of proximity to or contact with other items, without having information about the action that is being performed on them; in some cases that may be satisfactory (one can identify grooming easily, for instance, or larval tending) but it does not give information about the pattern of interactions, such as which behaviour immediately follows which. On the other hand image analysis systems can include information about movements, but it is difficult to make them both accurate and sophisticated enough to distinguish tasks very finely. Image analysis seems a promising way forward, since the cost of automatic data gathering and computation is continually and rapidly falling whereas the cost of human data gathering is, if anything, increasing. More to the point, questions about the mechanisms of short-term task allocation probably need the much finer-grained temporal sampling of continuous video. Nonetheless, which solution is preferable in any given case will always depend entirely on what information is sought.

7.3.2 General recommendations

Modelling

To summarise section 7.2.2, there is a need for a better modelling of the information available to workers. A paradigm for modelling that might be useful is to assume that each worker gauges the priority of the stimuli that it encounters (and indeed priority may be affected by *not* encountering the stimulus, as with food), and performs the task with the highest priority. It would then be necessary to find the correct way of modelling both the stimuli encountered and the rules that translate stimuli into priorities. For instance, some workers may have an innate tendency to give certain tasks higher priority, leading to a tendency to specialise which is nonetheless reversible according to conditions. The key is to balance the emphasis on understanding individual decision rules with that on understanding what information is encountered. Such a paradigm

would allow the integration of local and global stimuli, as well as the integration of tasks whose priorities depend on their associated stimuli in differing ways.

Yet questions must be asked about the extent to which integration should be pursued. It is true that social insect workers must integrate all these different types of stimuli, but is it appropriate for us to attempt to do the same when we do not yet understand how any one type of stimulus is treated? It may be better for the time being to pursue different cases separately, which is why the observation made of many models that they are limited to certain situations should not be taken as a *strong* criticism, so much as a limitation that must be borne in mind.

Experimentation

Experimenters need to do more to test models. This is hardly a fair criticism, since there has so far been little in the way of sensible (or at least easy) predictions to test. It is to be hoped that better links will be formed between models and experiments (and between modellers and experimenters), improving both.

In more specific terms, an urgent need is to find a good model system for studying short-term task allocation within the nest. The ant species *Leptothorax albipennis*, used for the studies in Chapters 5 and 6, is a good experimental subject in a number of ways, notably its moderately small colony size, ease of culture in the laboratory, and its natural preference for thin, flat nesting sites which is perfectly matched by a laboratory nest made of two glass slides held very close together.

It is nonetheless difficult to study short-term task allocation in the species with currently available techniques. Whilst the laboratory nests are excellent for observation, they are less effective for manipulating conditions within the nest (except, as described above, when it is colony composition that is manipulated in order to study long-term task allocation). The ants are quite sensitive to physical disturbance (especially vibration), but more seriously, to changes in gas composition such as those caused when part of the nest ceiling is lifted briefly and replaced (personal observation; see also Cox & Blanchard, 2000). Physical access to perform manipulations within the nest is therefore very difficult. The technique used in Chapter 5 of moving magnetic material using a magnet held outside the nest is effective insofar as the magnetic field does not appear to cause disturbance, but the manipulations that can be performed therewith

are very crude. Moderate progress might be had from manipulations outside the nest (such as to food supply) which change the balance of task allocation also within the nest (such as among food receivers, food storers, and larval feeders), as an indirect way of manipulating within-nest task demand.

7.4 Conclusion

In this work, I have argued that social insect task allocation occurring in the short-term and involving small groups is not the same as that occurring over the longer term or with large numbers, and that it needs to be studied separately (though not in isolation). Its proximate mechanisms are not well understood. I have presented theoretical and empirical studies which attempt to redress this lack. These have, I believe, made some small contribution, as well as providing lessons both positive and negative about effective ways to tackle the subject. However, they can but scratch the surface, and I hope in the future to see the emergence of a much clearer understanding of the mechanisms of short-term task allocation in small societies. I should be even happier if some of the lessons learned thereby prove to inspire engineers of human-generated agent societies.

Appendix A

Limits of parameter q in learning/forgetting function

The propensity π_i for task i is a probability and consequently must not exceed 1 or fall below zero. The function governing changes in π_i is

$$\Delta\pi_i = f(x, a, b, q) = \frac{(x-a)(b-x)q}{b-a} + (b-x)q^2, \pi_i = x.$$

The parameters a and b are chosen such that $0 \leq a \leq 1$ and $0 \leq b \leq 1$, $b \neq a$, and either $a \leq x \leq b$ or $b \leq x \leq a$. We wish to guarantee that

$$0 \leq f(x, a, b, q) \leq b - x \qquad \forall x, a, b : 0 \leq a \leq x \leq b \leq 1 \qquad \text{(A.1)}$$

and

$$b - x \leq f(x, a, b, q) \leq 0 \qquad \forall x, a, b, : 0 \leq b \leq x \leq a \leq 1 \qquad \text{(A.2)}$$

which is to say that when the function is used to increase propensities, we ensure that b is greater than a, and $f(\pi_i, a, b, q)$ should be positive but never so large that

$\pi_i + f(\pi_i, a, b, q) > b$; and when it is used to decrease propensities, we ensure that a is greater than b, and $f(\pi_i, a, b, q)$ should be negative but never so negative that $\pi_i + f(\pi_i, a, b, q) < b$.

If $q > 0$ then it can be seen that

$$\forall(x, a, b) : 0 \leq a \leq x < b \leq 1,\ a \neq b, \quad f(x, a, b, q) > 0\ ,$$

and likewise that

$$\forall(x, a, b) : 0 \leq b < x \leq a \leq 1,\ a \neq b, \quad f(x, a, b, q) < 0\ .$$

It can also be seen that $f(x, a, b, q) = 0$ when $x = b$. (See Figure 3.2 on p. 55 for an illustration of the form of the function.)

Differentiating $f(x, a, b, q)$ with respect to x, we have

$$\begin{aligned} f'(x, a, b, q) &= \frac{\mathrm{d}}{\mathrm{d}x}\left(\frac{(-x^2 + bx + ax - ab)q}{b - a}\right) - q^2 \\ &= \frac{(-2x + a + b)q}{b - a} - q^2 \end{aligned}$$

Taking first the case where $a < b$, the derivative is a decreasing function of x when q is positive. There exists a function $g(x) = b - x$ such that the condition in Expression A.1 holds as long as $f(x, a, b, q) \leq g(x)$ when $x \leq b$. At $x = b$, the two functions are equal and zero, and $g'(x) = -1$. If $f'(x, a, b, q) \leq -1$ at this same point $f(x, a, b, q)$ will not exceed $g(x)$ below $x = b$, as its derivative increases (becomes less negative) when $x < b$. The critical value of q can therefore be found by taking $f'(x, a, b, q) = -1$ with $x = b$ and solving for q:

$$\begin{aligned} f'(b, a, b, q) &= \frac{(-2b + a + b)q}{b - a} - q^2 \\ &= -q^2 - q \\ &= -1 \end{aligned}$$

so

$$q^2 + q - 1 = 0.$$

Applying the quadratic formula, $q = (-1 \pm \sqrt{5})/2$. We have already specified that $q > 0$, and at $x = b$, $f'(x, a, b, q) = -q^2 - q$; by plotting $-q^2 - q$ as a function of q it is clear that the behaviour required from $f(x, a, b, q)$ will be had with q between 0 and $(-1 + \sqrt{5})/2$ which is approximately 0.618.

The same argument can be applied when $b < a$ by replacing 'the derivative is a decreasing function of x' with 'the derivative is an increasing function of x', 'below $x = b$' with 'above $x = b$', and 'when $x < b$' with 'when $x > b$', leading to the result that Expression A.2 holds when $0 < q \leq (-1 + \sqrt{5})/2$.

Appendix B

"The Dynamics of Specialization and Generalization within Biological Populations"

This paper published by Spencer *et al.* (1998), an exploratory study of the model described in Chapter 3, is reproduced on the following pages. N.B. although the issue in which it appeared was published as *Journal of Complex Systems*, it was retrospectively renamed as *Advances in Complex Systems*.

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The Dynamics of Specialization and Generalization within Biological Populations

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ABSTRACT. We develop an abstract model to explore specialization and generalization in task performance by individuals within biological populations. Individuals follow simple rules of increasing and decreasing task propensities that could, for example, be based on learning and forgetting. The model does not explore efficiency per se, but makes the prediction that where behavioural specialization occurs in nature, organisms are likely to be reaping sufficient benefits from improved handling efficiency to offset the costs of increased search time. A second prediction is that among specialists, there will be a trade-off between stability and responsiveness. The model reveals potential similarities between a wide range of complex biological systems.

KEYWORDS: Specialists, generalists, simulation model, predation, pollination, switching, task allocation, search image, ants, bumblebees, social insects.

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1. Introduction

One of the greatest contributions of evolutionary biology is recognizing the importance of the uniqueness of the individual (Medawar, 1957). Indeed much of our understanding of evolutionary change through natural selection is associated with genetic biodiversity within populations (Ridley, 1993). However, both nature and nurture contribute to the uniqueness of individuals. Individuals within a population have different genotypes which encounter different environmental influences and such so-called genotype by environment interactions (Falconer, 1981) amplify phenotypic diversity. The most labile and hence arguably the most interesting aspect of phenotypes is behaviour. Here we will focus on behavioural diversity within populations by considering how learning may lead to generalization and specialization and how specialists may switch. These are important considerations over a surprisingly broad range of biological examples.

In ecology, for example, the stability of communities may be greatly influenced by individual predators specializing on one or a subset of many possible prey types (MacArthur, 1955; May, 1973; Pimm and Lawton, 1977). For example, if predators form search images for the more abundant of two (cryptic) prey types they may continue to hunt that prey type disproportionately even when it has become less abundant than the alternative (Begon *et al.*, 1990). Here population dynamics would be linked with the dynamics of individuals learning and forgetting certain search images. Similar reasoning can be applied to the behaviour of pollinators in which members of the same population may specialize in visiting only a subset of accessible flowers (Heinrich, 1979).

The advantage of specialization by individuals within groups is also considered to be of overwhelming importance in many of the major transitions in the evolution of life (Maynard Smith and Szathmáry, 1995). One such transition is from single-celled to multicellular organisms; another major evolutionary transition is from solitary organisms to highly social ones. The selective advantage of multicellular organisms over single-celled organisms is probably associated in part with cellular specialization leading to an efficient division of labour (Maynard Smith and Szathmáry, 1995). (Implicit in the division of labour is that individuals become more efficient as they specialize (Smith, 1776).) The evolutionary transition from solitary organisms to highly integrated societies of individual organisms (e.g. colonies of ants, termites and certain bees and wasps) is also associated with efficiencies that accrue from a division of labour and task specialization. Social insect colonies have been compared to factories within fortresses (Oster and Wilson, 1978, p. 21-23) and there are many different tasks that workers must perform, from building the nest and guarding the colony to tending the queen, rearing many different stages of brood, and feeding and grooming one another.

Several authors have modelled the association between learning and task allocation in social insects. Deneubourg *et al.* (1987) look at the influence of learning on the spatial fidelity of ants during foraging bouts, and discuss its implications for the division of labour. Using a conceptually similar model to our own, Plowright and Plowright (1988) model the emergence of "elitism" (i.e. that a small number of individuals do a disproportionate amount of the colony's work). More recently, Theraulaz *et al.* (1998) investigate the effects of variable response thresholds of individuals to tasks (see Discussion).

In diverse areas of biology, transitions from generalized behaviour to specialized behaviour are of major evolutionary importance. Clearly, there are fundamental differences, that must not be overlooked, between the systems we have just described. For example, individual predators will specialize on particular types of prey for their own immediate benefit, whereas cells within an organism, or ants within a colony, may specialize for mutual benefit (favouring the selfish genes they have in common). In other words, specialization within organisms or societies occurs because the entities involved belong to a community of mutual interest (Cosmides and Tooby, 1981; see also Bourke and Franks, 1995) and co-operate to favour their self interest indirectly, whereas specialization within ecological populations of distantly related individuals occurs due to direct self interest. Recognizing such fundamental differences should not, however, obscure key similarities in the dynamics of specialization and switching. It is these similarities that we explore here, by considering a model that investigates the dynamics of specialization within populations.

2. The Model

In outline:

1 Agents encounter one or more tasks in their environment.
2 At each time step each agent may perform one task.
3 If it performs a particular task its propensity to perform that task increases.
4 If it does not perform a task its propensity for performing the task decreases.

In detail:

Tasks are abstracted as discrete items, one task item being defined as the amount of task that one agent can complete in one unit of time. Hence we have not modelled the effects of changing task efficiency. For simplicity and generality, we have not specified time scales. All the parameters of the model scale with the

time step. The reason for this is that time scales for different organisms are likely to differ over several orders of magnitude, and the time period represented by one time step must reflect the behaviour under consideration.

Space is not modelled explicitly; instead, each agent experiences a probability, P, of encountering a task item during each time step. This probability is defined as

$$P = \frac{T}{(T + \alpha)} \tag{2.1}$$

where T is the total number of task items within the simulation, and α is a parameter relating the size of the arena within which the agents and tasks exist to the physical size of a task item and the area searched by an agent within one timestep. This provides a reasonable approximation for the situation where individuals and task items are distributed randomly within an arena of fixed size. At each time step, each agent has a probability P_n of encountering an item of each task, n, such that

$$P_n = \frac{T_n}{(T + \alpha)} \tag{2.2}$$

where T_n is the number of items of task n within the simulation.

At the start of the simulation, each individual has the same propensities for carrying out each specific task. These propensities represent the probability that, on encountering an item of task x, the individual will work on that task item. If an individual's propensity for carrying out task x is defined as π_x, then when the individual encounters an item of task x it has probability π_x of working on that item.

If a task item is worked on by an agent, the task item disappears from the simulation for all future time steps, and the individual's propensity for that task is increased by

$$\Delta\pi_x = \pi_x(1 - \pi_x)\lambda \tag{2.3}$$

where λ is the parameter governing the individual's "learning rate". Simultaneously, for all tasks n other than x, the individual's propensity decreases by

$$\Delta\pi_n = -(\pi_n(1 - \pi_n)\phi + \pi_n\phi^2) \tag{2.4}$$

where ϕ is the parameter governing the individual's "forgetting rate".

Thus if an individual performs a task, it becomes $\Delta\pi_x$ more likely to perform that task should it encounter it in the next time step, and it becomes less likely

to perform every other task by $\Delta\pi_n$ where π_n is its previous propensity for that task.

Task choice is determined purely by individual task propensities that are adjusted according to task experience. However, it is essential that a mechanism should exist to prevent task propensities from becoming trapped at zero. For the types of situation we model here, stochastic effects mean that, in time, individuals will always fail to encounter any given task for a long enough period of time that their propensity for that task reaches zero. Once a propensity has reached zero, the individual will never perform that task and so there will be no potential for its propensity to increase again. Unless individuals can be assured of a constant supply of a task for which they have high propensity, they must become prepared to do tasks which they would at first refuse if faced with a persistent dearth of their 'preferred' task(s).

We incorporate such a mechanism into this simulation by allowing individuals' propensities for all tasks to approach a low but non-zero 'resting level', R, on each occasion that a task item is refused. On refusal of a task item, for all tasks n,

$$\Delta\pi_n = -\left(\frac{(\pi_n - R)(1-\pi_n)\phi}{1-R} + \frac{(\pi_n - R)\phi^2}{1-R}\right) \tag{2.5}$$

if $\pi_n > R$, or

$$\Delta\pi_n = \frac{\pi_n(R-\pi_n)\phi}{R} + \frac{(R-\pi_n)\phi^2}{R} \tag{2.6}$$

if $\pi_n < R$.

In the model, the relationship between propensities and time is sigmoidal, given successive iterations of the equations 2.3, 2.4, 2.5 or 2.6. As a result, propensities change slowly when they are close to 1 or close to 0, but change more rapidly at intermediate values. We believe that this is biologically plausible, but other relationships might exist and are currently being explored.

3. Results

The principal factors that affect the behaviour of the simulation are the rates of learning λ(increasing propensity) and forgetting ϕ (decreasing propensity). To simplify this initial analysis we studied the dynamics of task allocation where only two tasks are present, and the learning and forgetting rates, λ and ϕ, are manipulated. Each simulation involves twenty initially identical individuals, and the following parameters were universal: resting propensity level, R, 0.2; rate

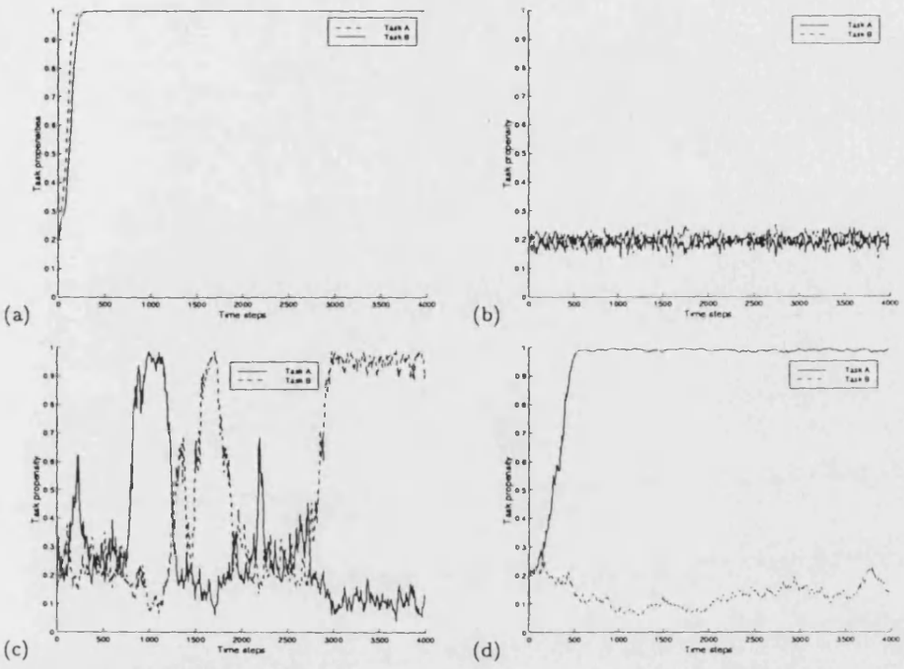

Figure 1. Individual task propensities against time for a range of learning (λ) and forgetting (ϕ) rates: (a) $\lambda = 0.199$, $\phi = 0.0066$; (b) $\lambda = 0.073$, $\phi = 0.1004$; (c) $\lambda = 0.199$, $\phi = 0.0752$; (d) $\lambda = 0.073$, $\phi = 0.0206$.

of task accumulation, 5 items per task per timestep; starting propensities, 0.2; density parameter, α, 50.

3.1. Individual behaviour

A range of individual responses to these conditions may be exhibited according to the values of learning and forgetting. When learning is rapid relative to forgetting, individuals exhibit behaviour such as that shown in Figure 1(a). The individual's propensities for both tasks rise rapidly and stabilise at close to 1, implying that the individual will perform almost every task it encounters. When individuals forget at a greater rate, as in Figure 1(b), their propensities for both tasks never increase significantly above the resting level of 0.2. These individuals rarely perform tasks of either type. In certain areas of parameter space, how-

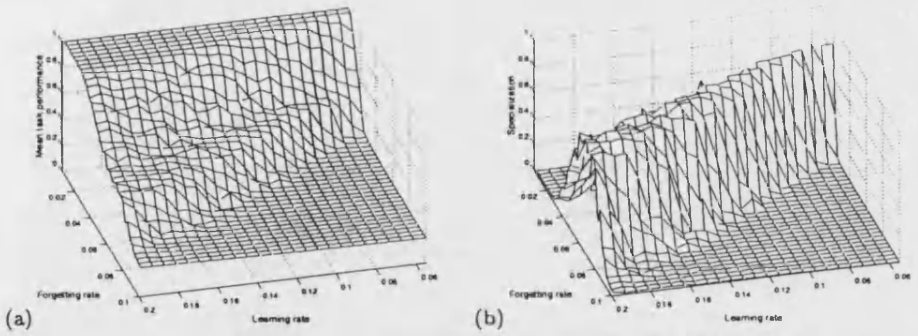

Figure 2. Collective responses across learning (λ) and forgetting (ϕ) parameter space. In both cases the z-axis represents mean values taken over the course of 500 timesteps, after the simulation had been allowed to run for 3500 timesteps. (a) Mean task performance, measured as the mean number of task items dealt with per agent per timestep. (b) Specialization, measured as the mean of the differences between each agent's propensities for the two tasks, $\frac{\sum_{i=1}^{n} |P_{i_A} - P_{i_B}|}{n}$ where n is the number of agents (equal here to 20) and P_{i_A} and P_{i_B} are the agent propensities for tasks A and B.

ever, individuals can specialise on one task for variable periods of time (compare Figure 1(c) with Figure 1(d)).

3.2. Population behaviour

Figure 2(a) shows the population average propensity for task performance as a function of the rates of learning and forgetting by individuals. The upper plane is characterised by learning rates that are high compared with forgetting rates; the general trend in this region is for agents to perform any task that they encounter (Figure 1(a) exemplifies individual behaviour under these conditions). The lower plane is characterised by learning rates that are lower or only moderately higher than forgetting rates; the general trend in this region is for agents to perform very few of the tasks that they encounter (Figure 1(b) exemplifies individual behaviour under these conditions). In the transition zone between these two regions, intermediate states are found.

Figure 2(b) shows specialization (i.e. the tendency to perform one task more than the other) as a function of the rates of learning and forgetting by individuals (the parameter range for learning and forgetting is identical to that shown in Figure 2(a)). At one end of the specialization zone, that is when learning is slow, specialization tends to be stable (as exemplified by Figure 1(d)). At the other

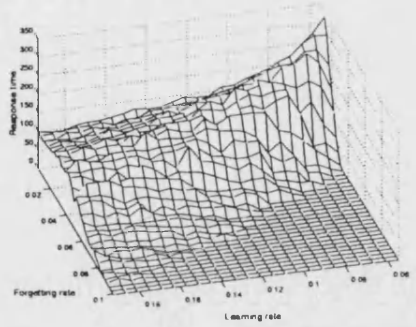

Figure 3. Collective responses across learning (λ) and forgetting (ϕ) parameter space. The simulation was run for 4000 timesteps with only task A present, at which point task B was introduced. The z-axis indicates the time taken before the rate (per agent per timestep) at which task B was performed approached (to within 0.2) the rate at which task A was performed.

end of the zone, where learning is fast, individual specializations are transient (see Figure 1(c)).

Figure 3 explores the ability of individuals within a population to respond to the introduction of a second task after a period in which they have encountered only one task. When the second task is initially introduced, none of the individuals in the group have encountered it previously and consequently they all have extremely low propensities for performing it. As they begin to encounter the second task, however, their propensities gradually increase until eventually the second task is performed at an equal rate to the first. The time taken to reach this point depends upon their learning and forgetting rates, and Figure 3 shows the time elapsed between the introduction of the second task and the point at which the second task is performed at a rate close to that of the first, across the same range of learning and forgetting rates used in Figure 2. This value is a measure of responsiveness: the shorter the elapsed time, the more rapidly individuals are responding to the change in conditions. However, it should be noted that the extremely low area of the graph associated with high forgetting rates is not indicative of a rapid response. This is because when individuals have a high forgetting rate they are incapable of learning even a single task (i.e. their propensities for the first task remain close to the resting level of 0.2); propensities for the second task were at the same resting level of 0.2 before its introduction and consequently little or no time elapsed before both tasks began to be performed at the same (very low) level. This graph shows that the ability to respond to change is associated with high values of both learning and forgetting.

4. Discussion

Our model shows that both generalization and specialization may occur in biological populations as a result of learning and forgetting, and that specialization is associated with a restricted range of parameter space. It further reveals a classic trade-off between stability and responsiveness.

Specialization is common in nature, both in the form of genetic predisposition or adaptation to a task, and in the form of behavioural specialization amongst potential alternative tasks. In this paper we examine the latter, which is much more labile allowing organisms to respond rapidly to their environment. Examples of behavioural specialization include prey specificity in predators (Begon *et al.*, 1990), flower specificity in pollinators (Heinrich, 1979), and task specificity in social insects (Hölldobler and Wilson, 1990; Bourke and Franks, 1995).

There are, however, costs to specialization due for example to increased search time (Krebs and Davies, 1993). Our model incorporates the effects of search time, since specialists 'waste' time steps rejecting task items. Figure 2 shows this cost of increased search time (the area of specialization in Figure 2(b) corresponds to the area of decreasing task performance in Figure 2(a)).

The costs of specialization beg the question why it is found so frequently in nature. One answer is that these costs may be offset by efficiency benefits through improved handling of tasks (Krebs and Davies, 1993). Since we do not model efficiency of task performance, this cost is not offset in our model. However, we can predict from our results that where behavioural specialization occurs in nature, organisms are likely to be reaping sufficient benefits from improved handling efficiency to offset the costs of increased search time.

The most likely cause of improved handling efficiency is learning (in the sense of skill refinement). Specialization will be favoured if individuals are not able to learn tasks concurrently, as can occur due to cognitive limitations. Specialization will also be favoured if the costs of learning a second task (incurred because time spent learning a second task is time that could be used to carry out a first task) are greater than the benefits. For simplicity, we have looked only at two tasks here, but the same principle applies wherever organisms are more efficient if they learn only a subset of possible tasks. A well-studied example of this is specialization among flower types by bumblebee foragers. Heinrich (1979) describes the way in which bumble bees learn to cope with different flower morphologies in the search for nectar and pollen. An interesting case, in which specialization is favoured by physiological as well as by behavioural adaptation to a task, is that of the digestive physiology of mallard ducks. It has been shown that these ducks have an increased digestive efficiency when they specialize on a particular food type (Miller, 1975, cited in Begon *et al.*, 1990).

Classical behavioural ecology models have shown, with respect to dietary breadth, that generalists should be expected to occur when the ratio of energy gained per unit handling time is the same for all items, or when search times are extremely long (Krebs and Davies, 1993). Such generalization may also be favoured when there is no significant cognitive limitation to learning tasks concurrently, or when there are no efficiency gains to be made through skill refinement.

Where specialization occurs, our model predicts a trade-off between stability and responsiveness. The population of agents (workers, predators or pollinators) can respond rapidly to the introduction of a new opportunity (task, prey species, flower type), but only if they have high learning and high forgetting rates (see Figure 3). The penalty of such behaviour is that such individuals will rarely specialize on one task for long. Typically they will flip stochastically from one task to another (see Figure 1(c)). In real biological situations this inconsistency would be likely to incur costs: efficiency gained from specializing and developing skills with certain types of item might be thrown away in too rapid switching to alternatives. The penalty of the opposite strategy (that is, stable specializations associated with lower learning and forgetting rates) is that in a changing environment, individuals will adjust their behaviour only slowly.

It is also notable that the area of parameter space where specialization occurs (Figure 2(b)) is also associated with slower responsiveness (Figure 3). This suggests that jacks of all trades, although they may be masters of none, are more likely to be successful opportunists.

There is very good evidence from both vertebrate and invertebrate predators for switching between prey types according to their relative density (Lawton *et al.*, 1974; Murdoch and Oaten, 1975; Murton, 1971; for review see Begon *et al.*, 1990, chapter 9). One traditional hypothesis for such behaviour is that predators form search images (Tinbergen, 1960; but see also Guilford and Dawkins, 1987; Giraldeau, 1997). The notion of a search image is that an organism forms a mental image of a cryptic prey type upon successive encounters and as a consequence tends to be less aware of other prey types. This implies that if the prey for which a predator has a search image becomes very rare, the search image is progressively forgotten, and also that search images are exclusive (a cognitive limitation).

There is also good evidence of switching behaviour in pollinators. Individual bees switch their preferences in response to changing relative abundance of flower types (Heinrich, 1979). For more recent work on bumble bee decision making during foraging, see Cartar (1992), Dukas and Real (1993), Dukas and Waser (1994). Rissing (1981) has shown that individual workers in seed harvesting ants also show preferences for particular seed types and switching behaviour. For

an example of switching behaviour in a non-social pollinator, see Goulson *et al.* (1997).

All of these examples emphasize the advantages of maintaining a specialization whilst a task remains available, and of being able to switch when circumstances change. The importance of individuals being able to respond to a changing environment suggests why in social insect colonies with workers that are physically polymorphic, the least specialized workers are always in the majority. In such cases, extreme physical castes are hard-wired for particular roles and therefore the ability of a colony to respond to a changing environment depends on having large numbers of generalists who can specialize behaviourally according to the needs of their colony (Oster and Wilson, 1978; Tofts and Franks, 1992; Bourke and Franks, 1995).

In solitary organisms, members of a population switch according to their own needs and local circumstances; in a population of workers in a eusocial colony switching can occur that benefits the entire community. If one viewed a colony of social insects exhibiting this trait, decisions might appear to be taken at a global level, but in reality this global behaviour is more likely to arise from independent, local decisions by individuals. An alternative model for social insects has been to consider individuals as having thresholds, which may be fixed (i.e. no learning—Bonabeau *et al.*, 1996) or variable (due to learning—Theraulaz *et al.*, 1998), and that there are global stimuli that emanate from each of the tasks. If the stimulus is greater than this threshold point, then every individual with a threshold below the stimulus performs the behaviour. By contrast, the model presented here has been based purely on local stimuli, and this has, we believe, given it an increased generality.

Our goal in this paper has been to explore in very general terms the dynamics of specialization and generalization in biological populations. In order to achieve some generality, we have deliberately kept our model simple. More specifically, we have excluded explicit spatial considerations in this first version of the model. (Clearly if different tasks, resources or prey types were spatially segregated and agents had restricted patterns of movement then tendencies to specialization could be greatly enhanced.) In the model, learning by the agents is a form of positive feedback and forgetting is a form of negative feedback, and hence our modelling can be seen as an exploration of stability versus responsiveness in terms of the relative magnitude of positive and negative feedback. The model is highly abstract, but for this very reason has revealed potential similarities among a wide range of complex biological systems.

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